

GEOLOGICAL HIERARCHIES AND BIOGEOGRAPHIC CONGRUENCE IN THE CARIBBEAN¹

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ABSTRACT

If it is agreed that an understanding of biohistory in some ways is tied to an understanding of geohistory, then one might also agree that what is needed is a precise means of specifying how a given biohistory is explicitly tied to a particular geohistory. The constraint in this type of analysis is the branching diagram, or cladogram, that permits a precise comparison of geographic area cladograms to demonstrate congruence between the cladistic message from biology with the cladistic message from geology. A proposal for identifying these cladistic constraints is given using a comparison of several different historical geologies of the Caribbean region as an example that contrasts with the constraints used by previous biogeographies in which an a priori notion of process, e.g., dispersal or extinction, was used to direct the outcome of biogeographic analysis.

Whether espousing dispersalism (Darlington, 1957) or vicariism (Croizat, 1958, 1962), biologists have always assumed that the distributions of organisms in some way reflect the nature of the world's geologic history. It was, thus, implied that an understanding of biohistory is tied to an understanding of geohistory. In the Darwinian-Darlingtonian tradition the relevant geohistory was assumed to be one of stabilism necessitating an interpretation of biohistory as one of active or passive dispersal. In other words, so long as the continents stood still something had to move to account for the occurrence of closely related organisms spanning large water gaps. Thus were invoked temporary land bridges suitable for crossing ocean barriers, birds with feet and feathers to which seeds and small animals would adhere during their transoceanic flights, and menageries supported on floating debris that was spewed into the ocean's currents from river mouths and deltas.

The difficulties inherent in these scenarios of a haphazard biohistory are apparent in Darlington's (1957) hypothesis that ostariophysans arose in central Asia and made their risky way along ephemeral freshwater routes to the southern continents without leaving a trace of these great migrations. But the hypothesis of a steadfast geography and a dancing biota was deemphasized after the theory of plate tectonics was elaborated.

Since most biologists had a penchant for believing that geologists had a special hold on the truth, the acceptance of continental drift caused some of these biologists to shift into reverse strat-

egy of proposing that it was the geography that moved while the organisms got carried about to their new longitudes and latitudes. Other biologists (Darlington, 1965; McDowall, 1971; Briggs, 1984) tried and still try to rescue the past by agreeing that the geography did in fact move but that the timing of these great events was wrong in relation to the ages of the biotas. Such attitudes might invoke the ages of fossils to show that all the taxa are too young to have been influenced by the geographic cataclysms. This view involves two assumptions, both wrong at some level: 1) that fossils can tell us how old a taxon is and 2) that the ages of the geologic events have been correctly assigned. The first assumption is wrong because fossils give a minimum rather than maximum age of a taxon, and the second assumption is put into question by recent age reassignments. For example, parts of the Caribbean which were originally supposed to have been moving along a transform fault at the moderate rate of 2 cm per year (Kellogg & Bonini, 1982) are now believed to be moving at the brisker pace of 4 cm per year (Sykes et al., 1982; Wadge & Burke, 1983), thus doubling the rate of motion and halving the ages of the events associated with translocation. But these relations leave us still at the mercy of general supposition when what is needed is some precise means of specifying that this biohistory is tied explicitly to that geohistory. This still unrealized need for precision is supplied by another conceptual revolution that, in terms of time spans involved in human intellectual history, might be said to have occurred more

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or less simultaneously in systematics and biogeography.

This revolution has been called cladistics, the science of character analysis and the use of branching diagrams. Its premises permit precise comparisons between biological and geological systems (e.g., Rosen, 1978). The general objective of cladistics is to discover congruence between the two that constrains historical explanation.

In the Darwinian tradition in biogeography it is dispersal that was the constraining concept, requiring an interpretation of the history of life in space contrary to what the data of life suggested. Leon Croizat (1958, 1962) was one of the pioneers who recognized that the biological data tell their own story, which can be at odds with a stabilist geology. Now that stabilist geology has been rejected in favor of a concept of mobilism, some biogeographers (Nelson & Platnick, 1981; Wiley, 1981) accept that biology has an independent story to tell about the history of the world. It is this independence of biological from geological data that makes the comparison of the two so interesting because it is hard to imagine how congruence between the two could be the result of anything but a causal history in which geology acts as the independent variable providing opportunities for change in the dependent biological world. The comparison becomes especially interesting if there is a congruence among geohistories based on different approaches to the geographic problem, and if there is a congruence among cladistic relations of different taxa with respect to the same geographic areas. The specific questions are: 1) do the members of different monophyletic groups of organisms have the same relations to each other with respect to geographic regions in which they are endemic and is their congruence with respect to these areas non-random; and 2) does this non-random congruence of different groups of organisms correspond to a branching diagram that represents part of the history of some geographic region? The constraint in these comparisons is the branching diagram rather than a process assumed to be of causal importance.

In 1976 and 1978 I suggested a history for the Caribbean land and water that, at a rather general level, is consistent with the present distributions of plants and animals in the region including the Antilles, Central America, northern South America, and the southeastern and southwestern United States. The 1976 proposal, which was

based largely on a descriptive history by Malfait and Dinkleman (1972) and Tedford (1974), was questioned by Pregill (1981) whose claim was that there is no geologic evidence warranting such a proposal. This claim was critically evaluated recently by Hedges (1982) who disagreed with Pregill on the grounds that ample geologic data had been available for some time in support of the Malfait and Dinkleman-Tedford theory (he cited 13 literature sources). Since the time of Hedges' reply to Pregill, I became aware of several other accounts of Caribbean history based on a variety of geologic data sources (Birnie, 1977: movement along major fault zones; Pindell & Dewey, 1982: plate contour matching and paleomagnetic data; Kellogg & Bonini, 1982: gravity data, seismic profiles, radiometric data, and earthquake data; Sykes et al., 1982: slip vectors of shallow earthquakes and other seismic data; Wadge & Burke, 1983: reconstructing plate motions by closing the Cayman Trough along its bounding transform faults). It is apparent, therefore, that Pregill was operating with a different set of constraints, namely, that the biota is recently distributed by means of dispersal. Hence, no number of geologic accounts or amount of data would be expected fundamentally to alter his position. My constraint is the cladogram and how it describes relationships of taxa and areas. What I propose is to divide the historical geology of the Caribbean into the minimum number of time periods in which different geologic theories agree on the geographic contacts between different areas and the severing of those contacts. In this way I have covered four main periods spanning 165 million years.

CARIBBEAN HISTORY

As I interpret the geological literature the following events took place in Caribbean geohistory; some prefatory remarks are in order.

There are two basic kinds of theories about the history of the Caribbean: 1) those of Salvador and Green (1980) (Figs. 1–9) and Anderson and Schmidt (1983) (Figs. 10–16). These describe a north–south expansion of the Gulf-Caribbean region by the latitudinal displacement of North and South America. Both of these are primarily pre-Cenozoic theories that focus principally on the opening of the Gulf of Mexico so that the detailed placement of the Greater Antilles is secondary in importance. 2) All remaining theories, as exemplified by (Figs. 17–29) Malfait and Dinkle-



FIGURE 1. The Gulf of Mexico and Caribbean region in the Kimmeridgian (143 Ma) according to Salvador and Green (1980). This, and Figures 2–9, is one of two pre-Cenozoic theories focusing primarily on the opening of the Gulf, and is based on the notion that the Caribbean, like the Gulf, was created by north–south spreading or separation of North and South America. It is distinguished by proposing an origin of Cuba from volcanism along a northern South American transform fault and the gradual shift northward toward the Bahama Bank of Cuba. Other Greater Antillean, and the Lesser Antillean components are also viewed as having in situ volcanic origins, although the Beata Ridge is depicted as a volcanic chain of which Hispaniola is the most northerly element. Black dots represent primary sites of volcanism. Vertical hatching is land; cross-hatching is shallow-water shelves with sedimentary deposits; heavy lines with half arrows are transform faults; and heavy lines with solid arrows are subduction zones. Only the main areas of volcanism are shown by the solid dots.

man, and Tedford (see Rosen, 1976), Pindell and Dewey (1982), Sykes et al. (1982) (Figs. 30–33), Wadge and Burke (1983), and Dickinson and Coney (1980) (Fig. 34), describe longitudinal displacement events of land and sea floor that are primarily Cenozoic and focus principally on the Caribbean heartland, particularly the origins and movements of the Antillean islands. Readers of these two kinds of historical geologies will notice immediately that the latitudinal expansion theories place the origin of the Greater Antilles along the northern edge of South America, not unlike the older theory of Vandell (1972), whereas the longitudinal displacement theories identify the main Antillean islands as part of an ancient island arc that connected northern Central America (Yucatan) with northwestern South America. Although seemingly contradictory theories of Caribbean history, the consequences of the two

theories in terms of the sequence of land connections and disconnections are similar. Their common elements include: 1) contact between North and South America via a proto-Greater Antilles; 2) Cenozoic longitudinal displacement of the Antilles; 3) hybridity of Hispaniola and contact of central Hispaniola with eastern Cuba; 4) approximation of eastern Cuba with Florida and western Cuba with northern Central America (Yucatan) at some stage; 5) secondary closing of the Central American, South American water gap; 6) motion of the Chortis block (Honduras and Nicaragua) along a transform fault (= Motagua-Polochic fault and Cayman Trench) with comparable motions of the Greater Antillean elements.

Although both theories accept a later origin for lower Central America connecting Honduras and Nicaragua with Colombia, in Pindell and Dewey



FIGURE 2. The Gulf of Mexico and the Caribbean region in the Berriasian (132 Ma) according to Salvador and Green (1980). At this stage some east-west translocation is postulated at the western margin of the Caribbean region (note the position of Honduras and Nicaragua, H-N, and compare with subsequent figures) although a north-south expansion is still considered primary.



FIGURE 3. The Gulf of Mexico and the Caribbean region in the Berremian (117 Ma) according to Salvador and Green (1980).



FIGURE 4. The Gulf of Mexico and Caribbean region in the Cenomanian (93 Ma) according to Salvador and Green (1980). Jamaica (J) is depicted as a consequence of submarine volcanism and Hispaniola is shown just to the east of Jamaica with a small subaerial component.

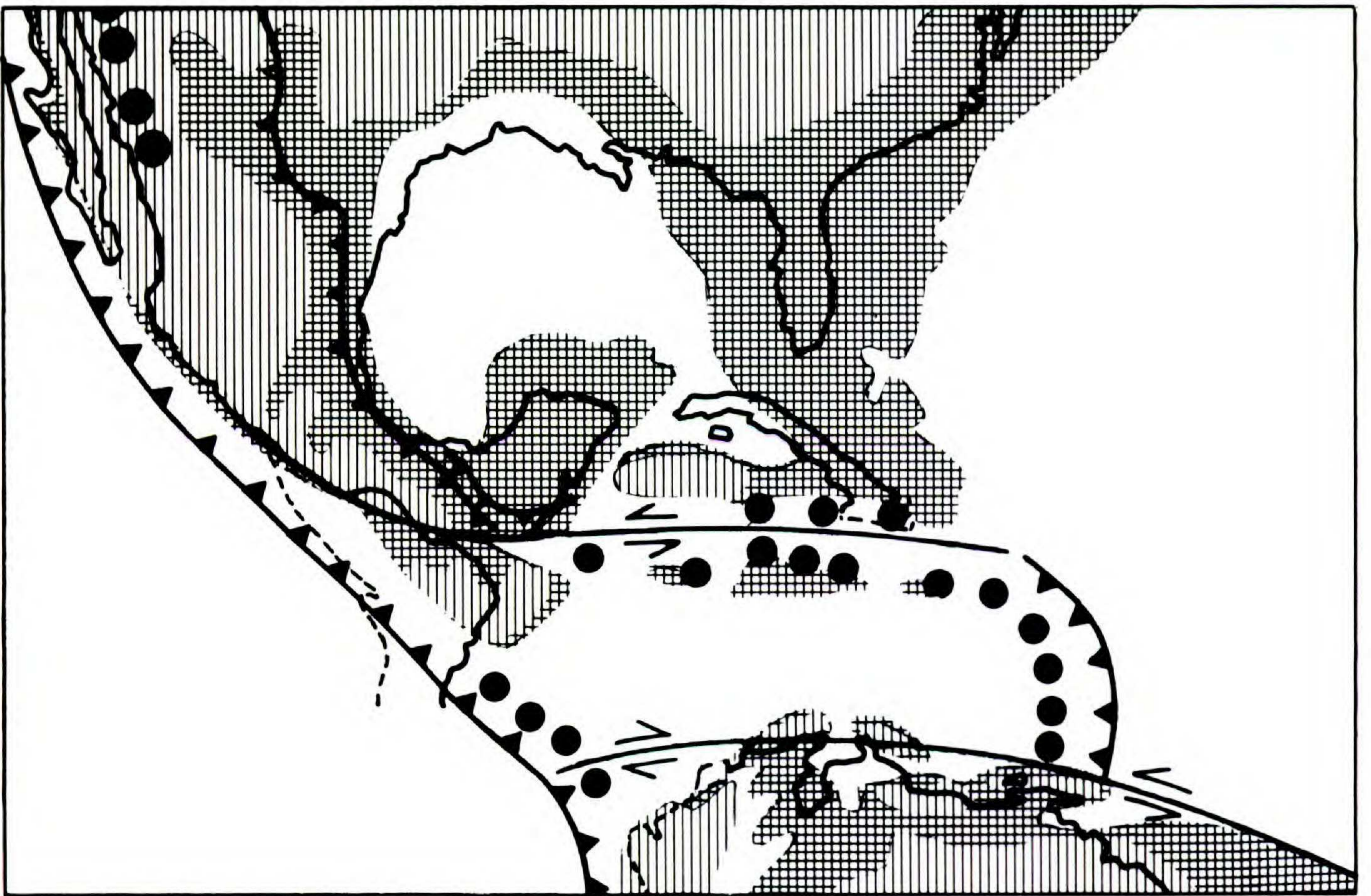


FIGURE 5. The Gulf of Mexico and the Caribbean region in the Maastrichtian (70 Ma) according to Salvador and Green (1980). The outlines of all of the Greater Antillean islands are now shown, with the western, subaerial part of Cuba (C) in contact with the Yucatan (Y) platform.

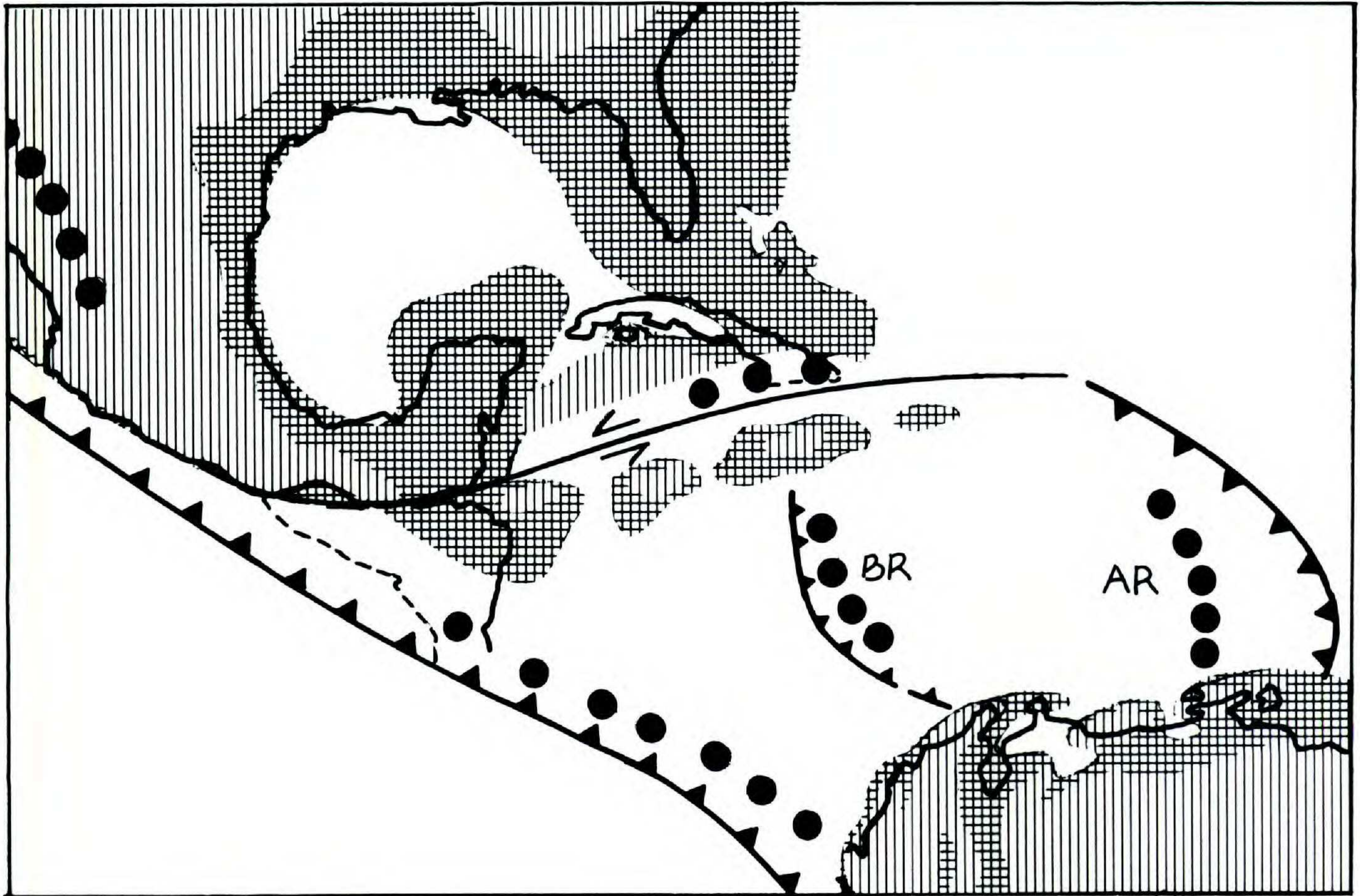


FIGURE 6. The Gulf of Mexico and the Caribbean region in the Paleocene (55 Ma) according to Salvador and Green (1980). The Beata and Aves Ridges (BR and AR respectively) are now emplaced and the Caribbean has undergone its maximum north-south expansion. A volcanic chain now extends between northwestern South America and the ultimate site of Honduras and Nicaragua.

ey's (1982) longitudinal displacement theory Honduras and Nicaragua (and by implication of polar position data, also Jamaica) had, along with Panama and Costa Rica, an older origin in the eastern Pacific and were emplaced as the proto-Caribbean/eastern Pacific sea floor was sucked into the Caribbean heartland. Thus, both kinds of theories include the potential for Antillean juxtaposition with northern Central America (Yucatan) at some time in their histories. The largest difference between them is how far east one should situate an island arc that joins northern Central America (Yucatan) with Colombia and in the ages and rates of motion of the Antillean components. But there seems little reason to argue that a single ancestral biota might have occupied large parts of what now are a series of isolated islands, thus providing major opportunities for biotic differentiation in a pattern of land connections and disconnections very much alike for both latitudinal and longitudinal displacement theories. From the standpoint of biogeography, then, the different theories disagree in some details and in focus, but agree in ways that concern biohistory.

HISTORICAL SUMMARY

150–165 MA

At this early stage North and South America were closely approximated, separated in what is now the Gulf region by the northern Central America (Yucatan) block, which later became the principal component of northern Central America (Yucatan). The Bahama platform lying due ESE of southeastern North America existed at this time. No elements of the Antilles would be recognizable at this period. Northern Central America (Yucatan), including southwestern Guatemala, Honduras, and Nicaragua, would, at this stage, be Pacific land (the Chortis block) lying to the southwest of what was to become Mexico. Africa, North America, and South America were all still in contact with a small piece of Africa lying athwart the southeastern segment of the already formed Appalachian chain and including Florida and the northern Bahamas. Major fault zones were beginning to form 1) to the north and south of northern Central America (Yucatan) in the Gulf region, 2) to the east, west, and south of the Bahama platform, the eastern part forming

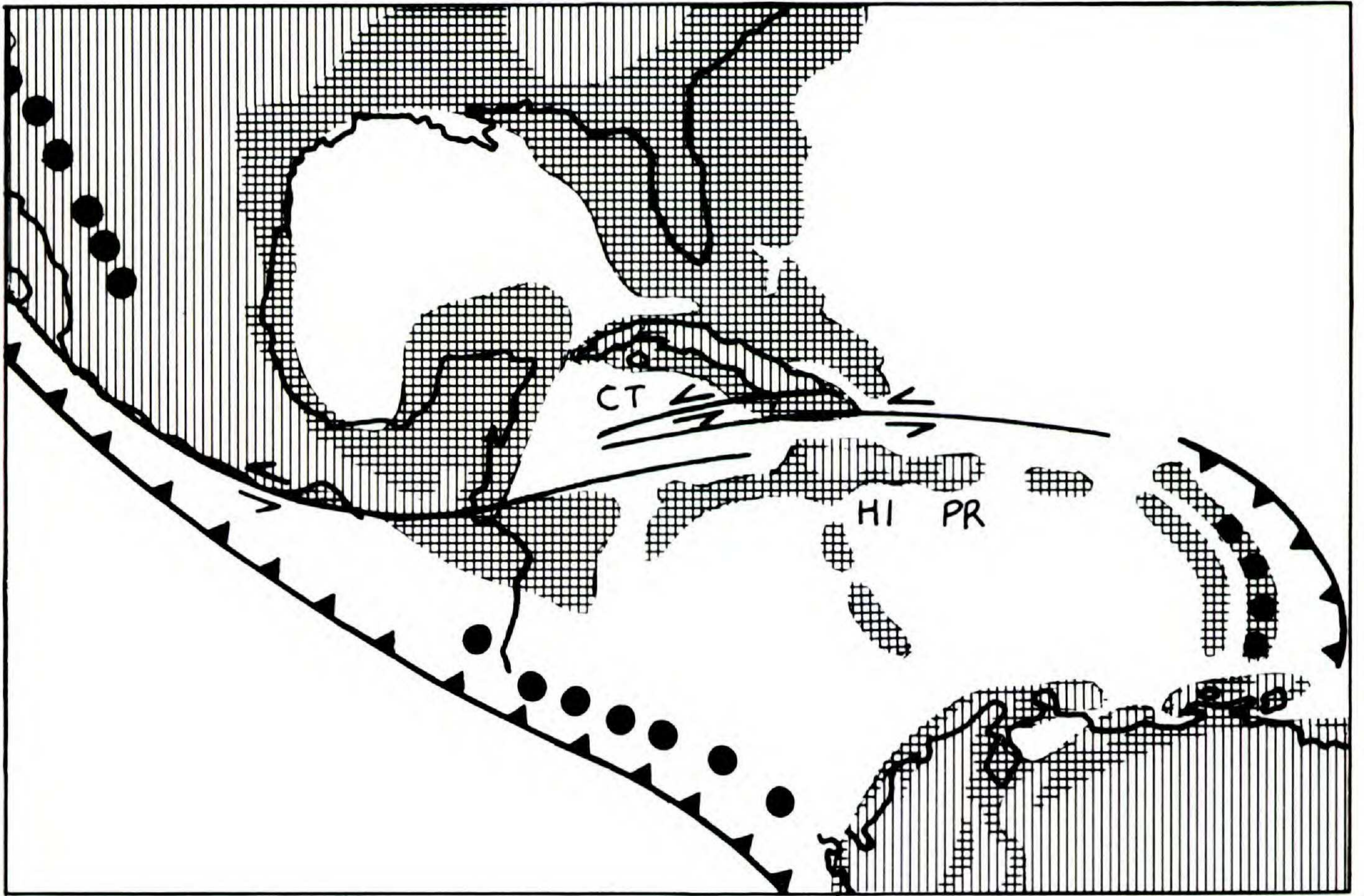


FIGURE 7. The Gulf of Mexico and the Caribbean region in the Middle Eocene (42 Ma) according to Salvador and Green (1980). A spreading center has now appeared in the Cayman Trough (CT), accentuating east-west translocation along the faults to the north and south of the Caribbean basin and the latter is being compressed by the motion of North and South America toward one another. In this model only Hispaniola (HI), Puerto Rico (PR), two sections of Cuba and the Isle of Pines are considered to be subaerial. The proto-Lesser Antilles have now appeared on the eastern border of the Aves Ridge.



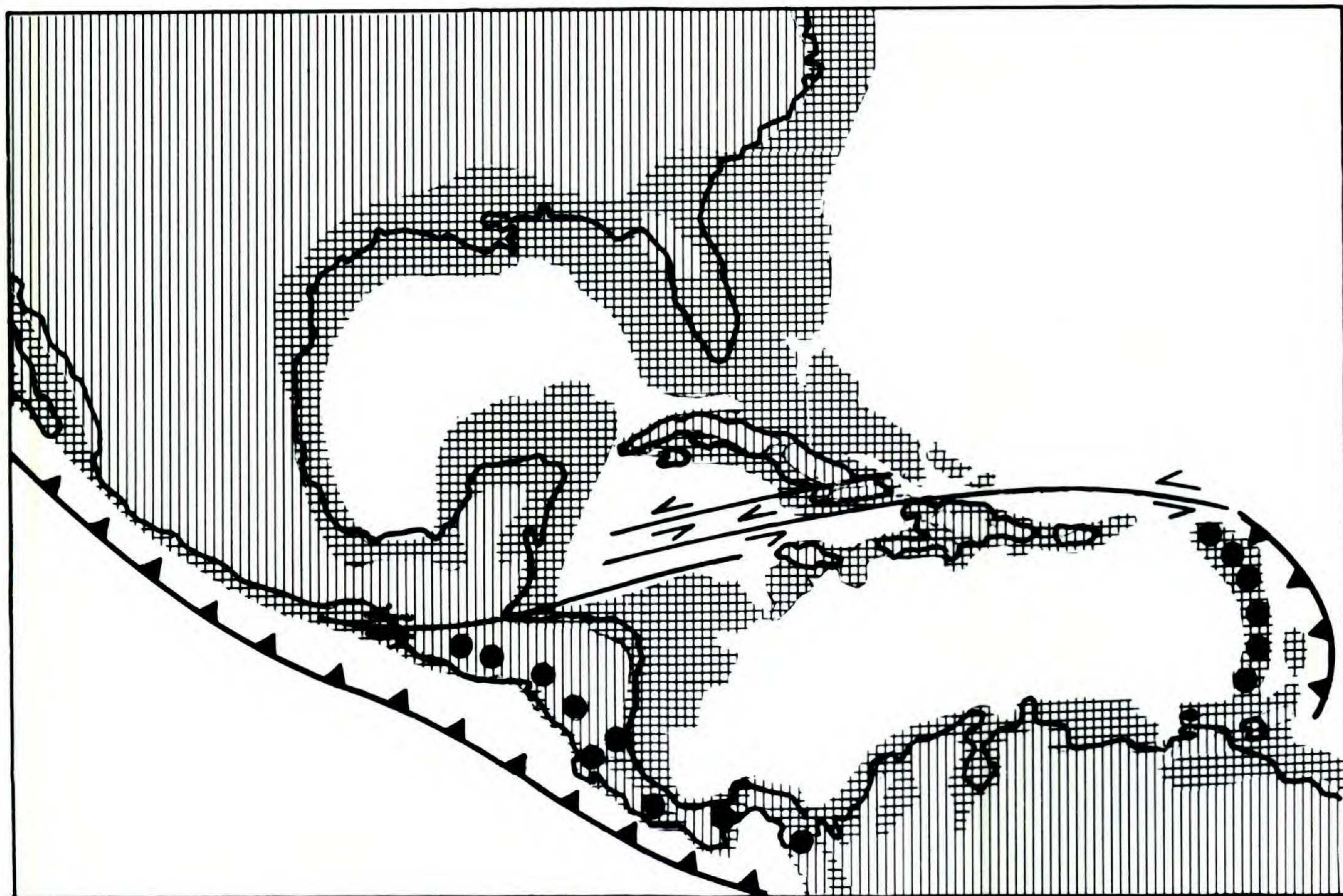


FIGURE 9. The Gulf of Mexico and the Caribbean region in the late Miocene (7 Ma) according to Salvador and Green (1980). The Caribbean basin has undergone nearly its maximum compression in relation to the Recent configuration, Cuba has consolidated into three sections, Hispaniola into two, and Jamaica and a major part of the Yucatan is subaerial.

a northern segment of the proto-mid-Atlantic ridge, 3) a southern segment of the proto-mid-Atlantic ridge between northeastern South America and the proto-Gulf of Guinea region of Africa, and 4) a major part of the western Central American Trench off the west coast of North America and South America.

95 MA

North and South America have now separated substantially, opening up the Gulf of Mexico and an area to the south that was later occupied by Caribbean sea floor. Northern Central America (Yucatan) has now become joined to Mexico, and the Chortis block has moved east to a position south of Mexico and west of northern Cen-

tral America (Yucatan), the area of contact representing the origin of the Motagua-Polochic transform fault (= Cayman Trough). A proto-Antilles island arc, of volcanic origin, has formed between northern Central America (Yucatan) and western South America, and the Central American trench in this region has jumped to the east of the arc to form the leading edge of a subduction zone that will enable the proto-Antilles to override the proto-Caribbean sea floor. The western end of this island arc moved north, where; colliding with northern Central America (Yucatan); Jamaica, the Caymans, and southwestern Hispaniola were sheared off from western Cuba. Thus, Jamaica, the Caymans, southwestern Hispaniola, and western Cuba all accreted respectively to the southern and eastern parts of north-

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FIGURE 8. The Gulf of Mexico and the Caribbean region in the early Miocene (21 Ma) according to Salvador and Green (1980). North-south compression of the Caribbean basin continues. Lower Central America begins to emerge and undergo compressional deformation, Puerto Rico and three components of Hispaniola are present and subaerial, and Cuba and the Isle of Pines include seven separate subaerial components. Northern Central America (Honduras-Nicaragua) is now emplaced, having migrated eastward under the Yucatan (Nuclear Central America) along the Polochic-Motagua extension of the Cayman Trough.

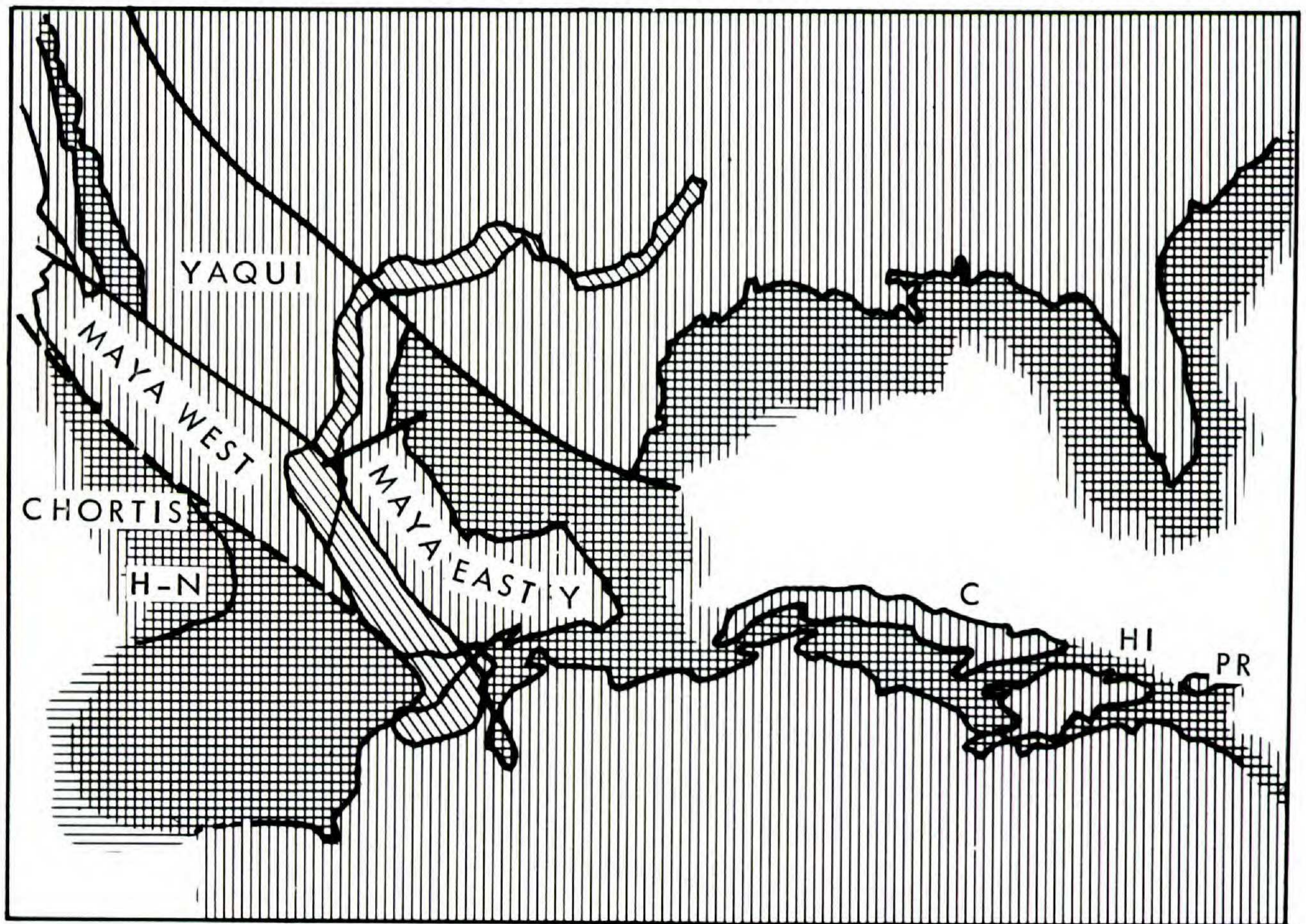


FIGURE 10. Post-Paleozoic to pre-Middle-Jurassic configuration of Middle America, the Gulf and Caribbean regions according to Anderson and Schmidt (1983). Vertical hatching is land, cross-hatching is shallow-water shelf, and oblique hatching is a reconstructed curvilinear belt of Paleozoic rocks that show lithologic and paleontologic similarities. The proposed positions of Yucatan (Y), Hispaniola (HI), and Puerto Rico (PR) are shown. This model also incorporates the notion that the region consisted of several microplates as labelled: Yaqui; Maya West; Maya East = Yucatan, in part; and Chortis = southern Guatemala, Honduras, and Nicaragua. Like the model of Salvador and Green (1980) this is a pre-Cenozoic description of the formation of the Gulf of Mexico and Caribbean by the north-south displacement of North and South America (see Figs. 11-17).

ern Central America (Yucatan). The attenuated Bahama platform made a southeastward approach to the northern South America trench, and the mid-Atlantic ridge is now well developed between Africa and North America, the former having left behind Florida and the small Appalachian segment mentioned above.

65 MA

North and South America have separated further along a modern north-south axis and the proto-Antillean arc had begun to stream eastward into the Caribbean heartland opened up by the separation of North and South America. The Oriente of Cuba is now situated to the east, con-

tacting the Bahama platform along its northeastern margin and nuclear Hispaniola to the south. Southwestern Hispaniola, the Caymans, and Jamaica have begun an eastward migration away from the southern edge of northern Central America (Yucatan), moving along the proto-Cayman trough, which has a complex structure including pieces to the north, west, and south of Cuba and a north-south arm southeast of the Bahama platform that is to become the leading eastern edge of the Caribbean plate. The Aves Ridge or proto-Lesser Antilles has formed just behind this leading plate margin. The Chortis block has also begun a southeastward migration along the Motagua-Polochic fault, carrying it closer to northern Central America (Yucatan),

FIGURE 12. The Gulf of Mexico and Caribbean region in the Middle Jurassic (150 Ma) according to Anderson and Schmidt (1983). As a result of latitudinal displacement of North and South America the proto-Greater Antilles are depicted as moving north away from South America.

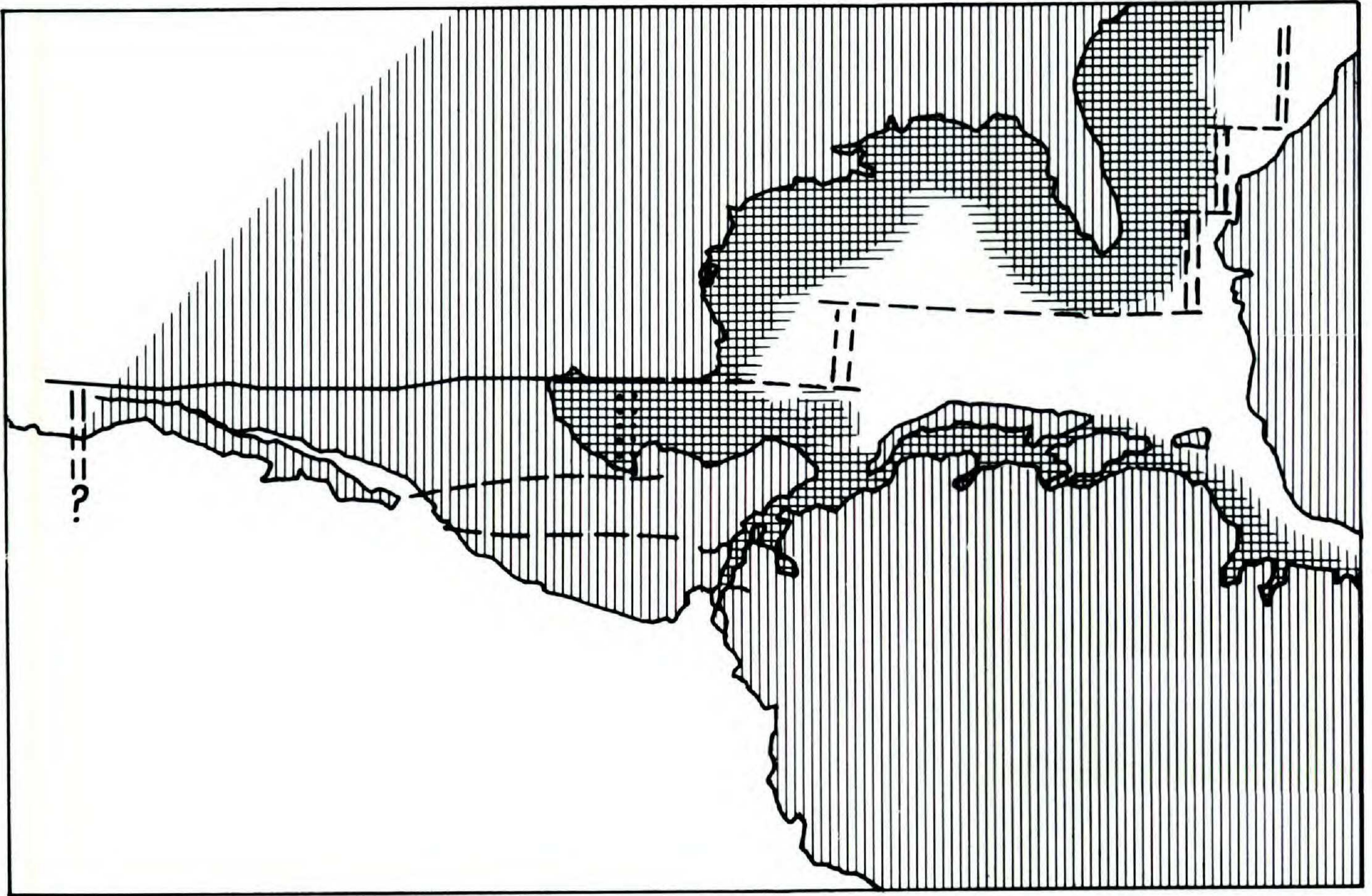
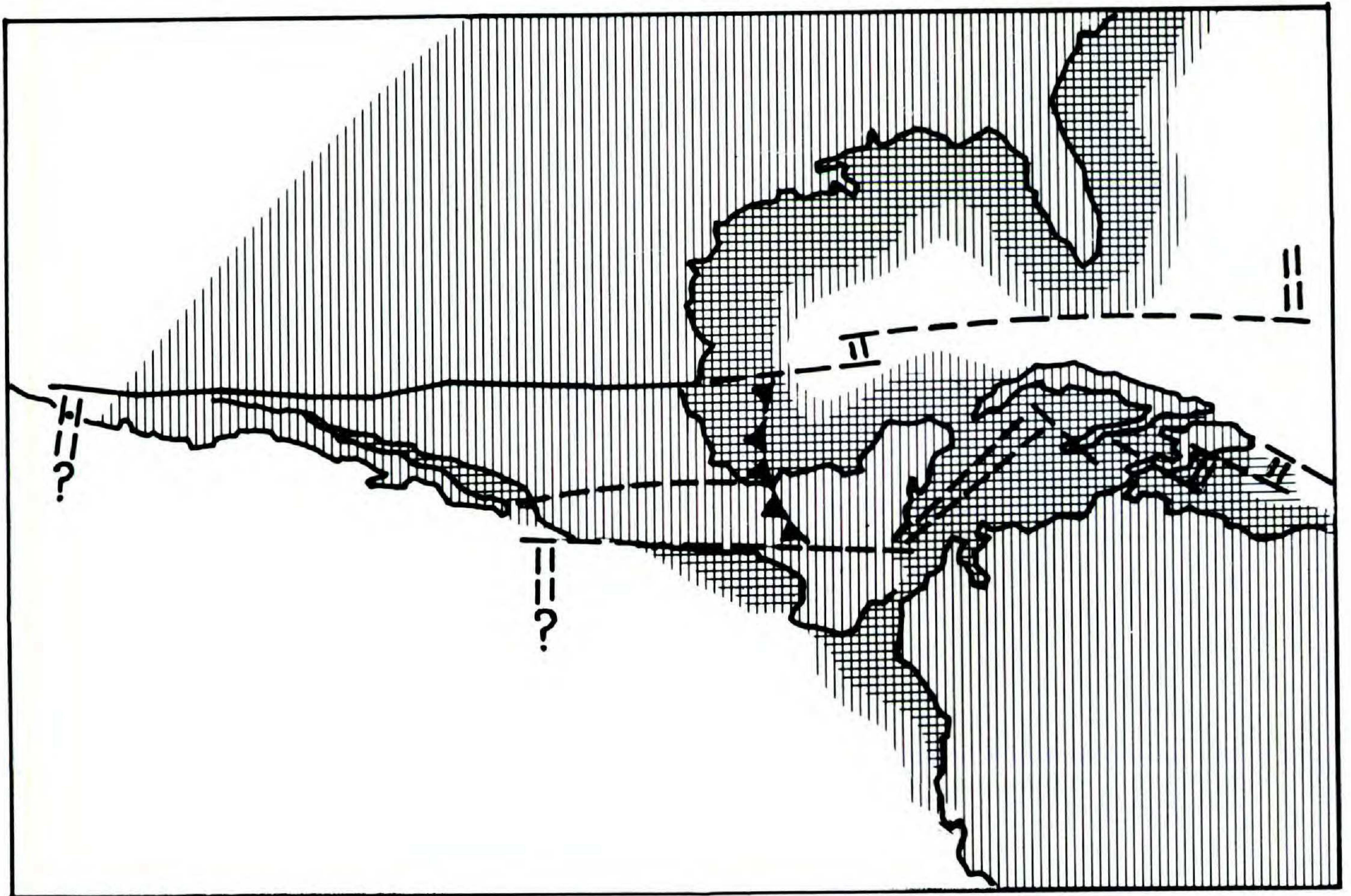


FIGURE 11. The Gulf of Mexico and Caribbean region in the Middle Jurassic (160 Ma) according to Anderson and Schmidt (1983). The proto-mid-Atlantic ridge can be seen between south-eastern North America and north-western Africa as a three-step inferred fault of broken lines. Vertical hatching is land, cross-hatching is shallow-water shelf, unbroken heavy lines is the original position of the Mojave-Sonora megashear that bounds the Yaqui microplate to the north (see Fig. 10), broken heavy lines are inferred faults.



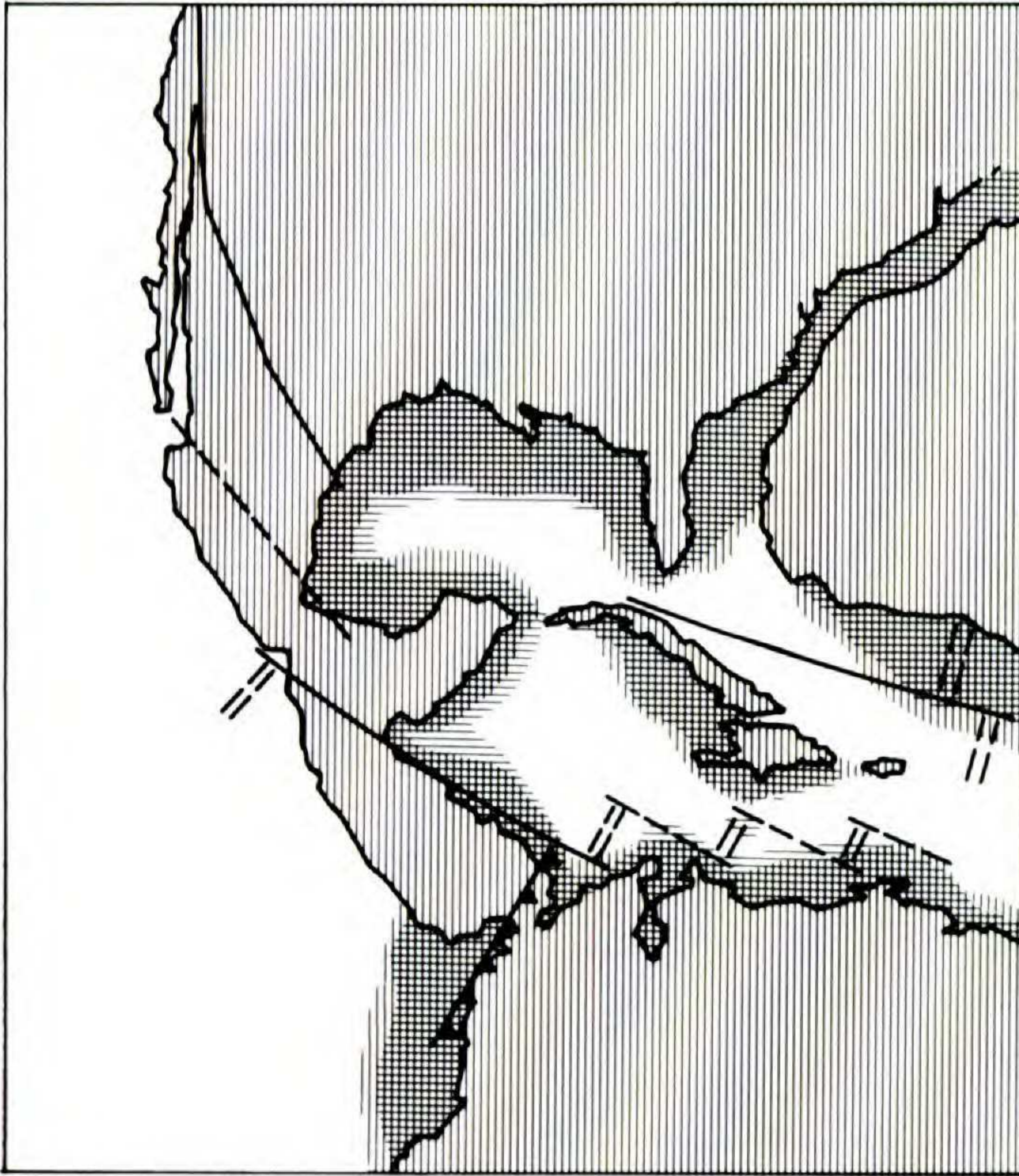


FIGURE 13. The Gulf of Mexico and Caribbean region in the Kimmeridgian (ca. 140 Ma) according to Anderson and Schmidt (1983). Compare with Figure 1.

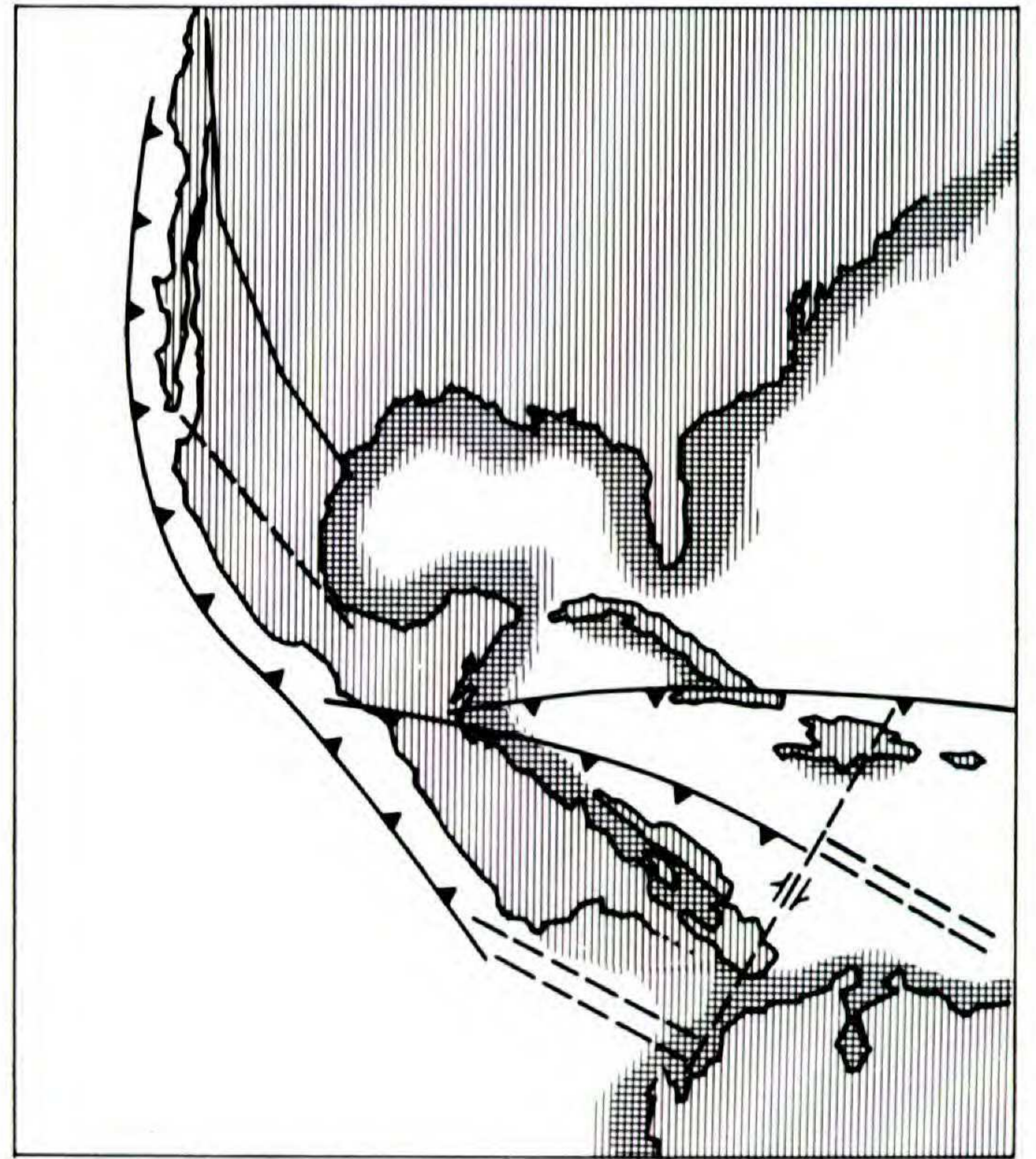


FIGURE 15. The Gulf of Mexico and Caribbean region in the latest Cretaceous (ca. 70 Ma) according to Anderson and Schmidt (1983). Latitudinal displacement is still continuing.

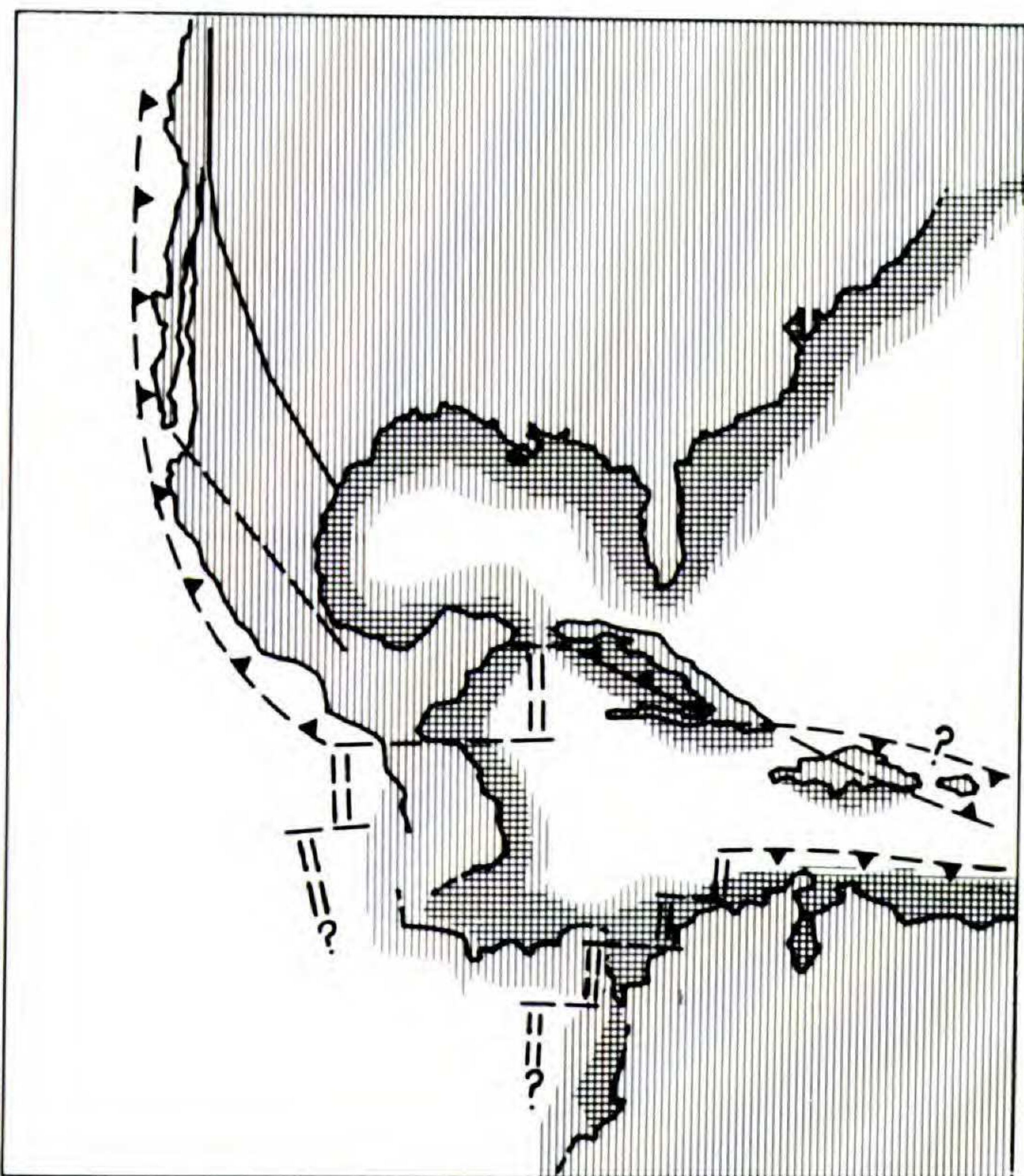


FIGURE 14. The Gulf of Mexico and the Caribbean region in the Late Cretaceous (ca. 95 Ma) according to Anderson and Schmidt (1983). In this reconstruction western Cuba has just made contact with the Yucatan and Bahama platforms. Compare with Figure 4.

and lower Central America has moved in from the eastern Pacific to suture with the Chortis block.

PRESENT TO 9 MA

During this pre-modern epoch in Caribbean history nuclear Hispaniola continued its eastward movement, separating from the Oriente of Cuba and being joined by southwestern Hispaniola (about 9 Ma) and picking up a small southern piece of the Bahama platform along its northern edge (about 3 Ma). Jamaica and the Caymans have trailed behind maintaining a steady distance from southwestern Hispaniola, so that, although at one time connected by contiguous land to Cuba and Hispaniola through northern Central America (Yucatan), the former islands have been isolated fragments for most of Caribbean geohistory (during which, the White Limestone Group of central Jamaica was continuously sub-aerial, Robinson, 1976; Robinson et al., 1977). Central America now occupies the site, formerly the province of the proto-Greater Antilles, and is joined to the precursor lands of western Colombia (the area of the Rio Cauca and Magdalena basins). The Cayman Trough has a complex configuration including a spreading center between its northern and southern slip-fault components.

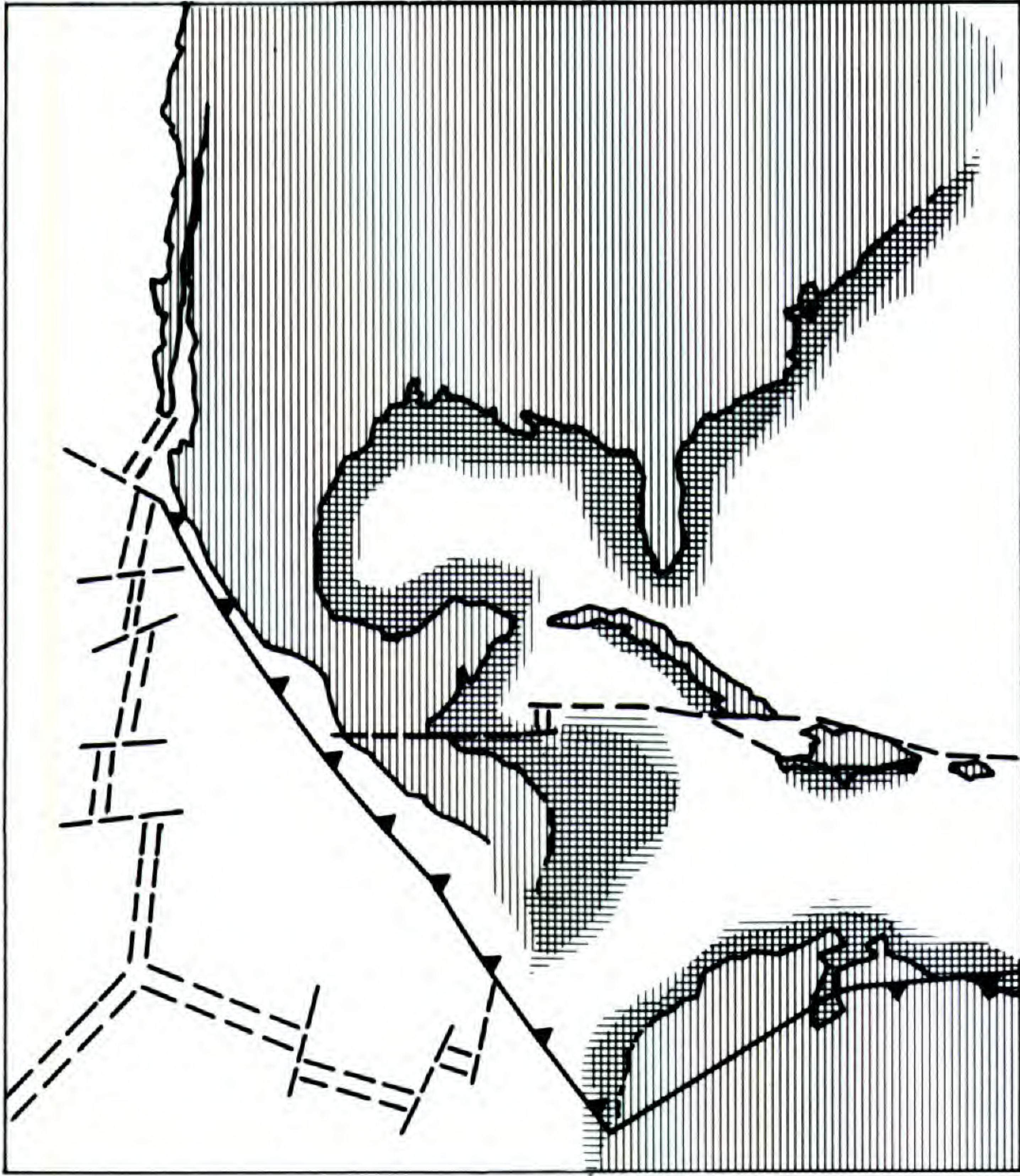


FIGURE 16. The Gulf of Mexico and the Caribbean region in the Miocene (ca. 8 Ma) according to Anderson and Schmidt (1983). Compare with Figures 8 and 9. Latitudinal expansion has ceased and northern Central America (Honduras and Nicaragua) remain isolated from northwestern South America.

The southern component is now continuous with the active Motagua-Polochic left-lateral transform fault, which connects with the again unbroken western Central Americas Trench. The northern component of the major Antillean trench system continues eastward between the Bahama platform and the formerly Bahamian section of northern Hispaniola and ultimately

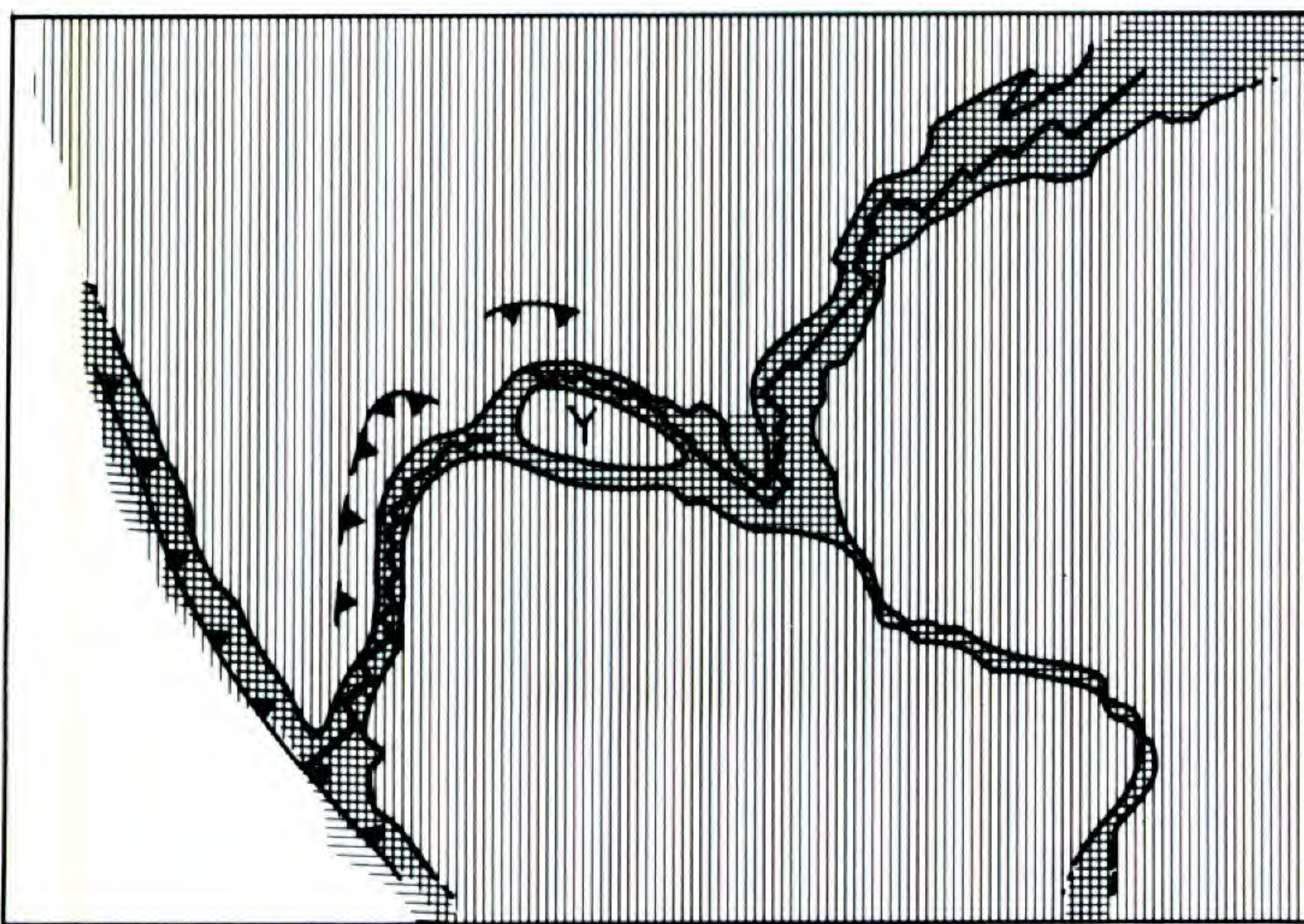


FIGURE 17. The Gulf of Mexico and the Caribbean region in late Pangaeian time (ca. 165 Ma) according to Pindell and Dewey (1982). Yucatan (Northern Central America, Y) is depicted here as a separate microplate between North and South America.

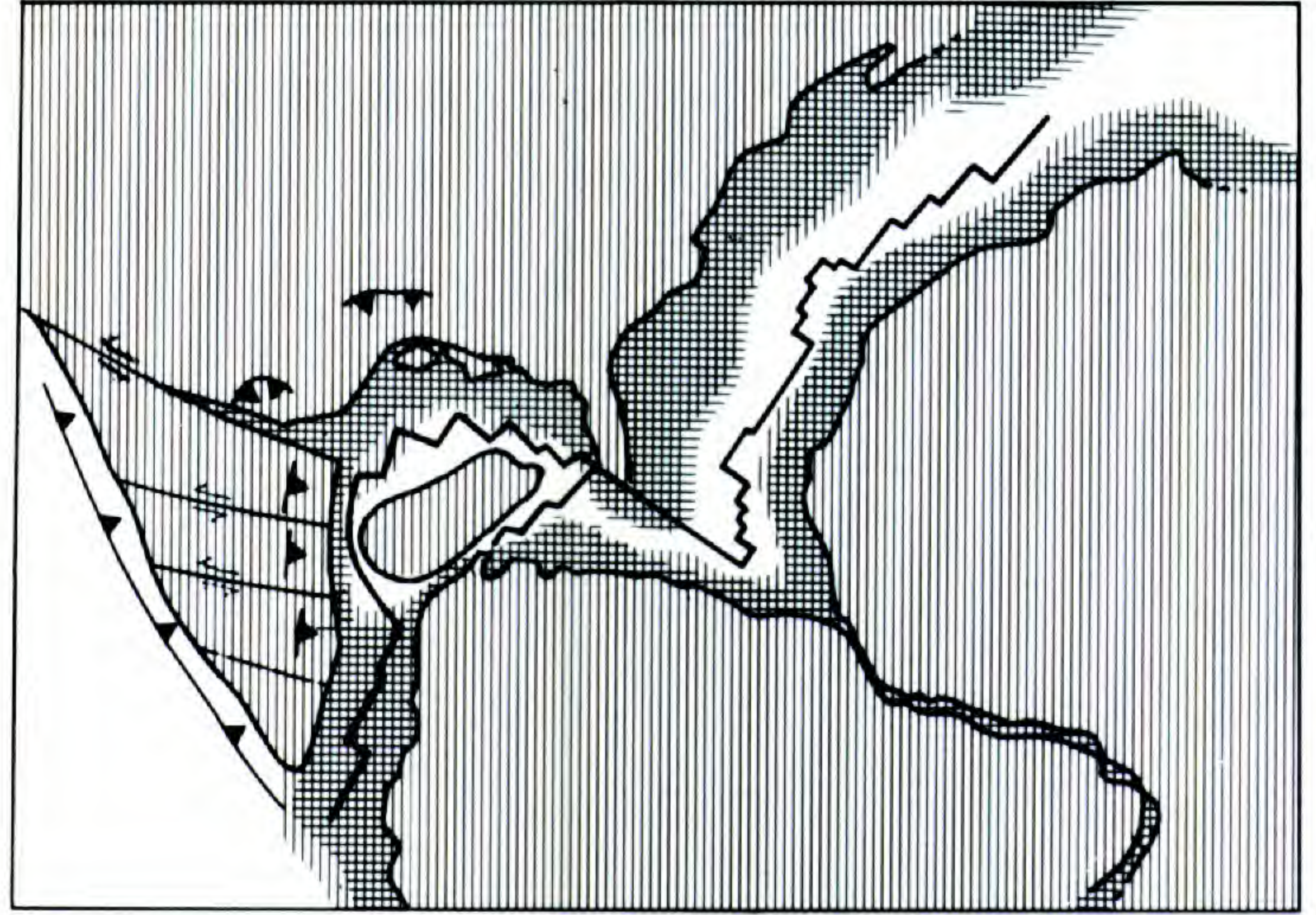


FIGURE 18. The Gulf of Mexico and the Caribbean region prior to the separation of Africa and South America (ca. 150 Ma) according to Pindell and Dewey (1982). The heavy east-west lines across Mexico are areas of thrusting that separate Mexico from southwestern North America at roughly the level of the Rio Grande and that subdivide Mexico into four discrete zones.

connects with the subduction zone along the leading eastern edge of the Caribbean plate behind which the modern Lesser Antilles have emerged as chains of volcanic stepping-stones from the precursor Aves Ridge. With the ultimate disappearance of the Cauca-Magdalena, transgressing seaway in northwestern Colombia, a new continuous land connection was made between North and South America.

HISTORICAL SUMMARY

To the extent that the foregoing account is correct, one can say that the Caribbean land and

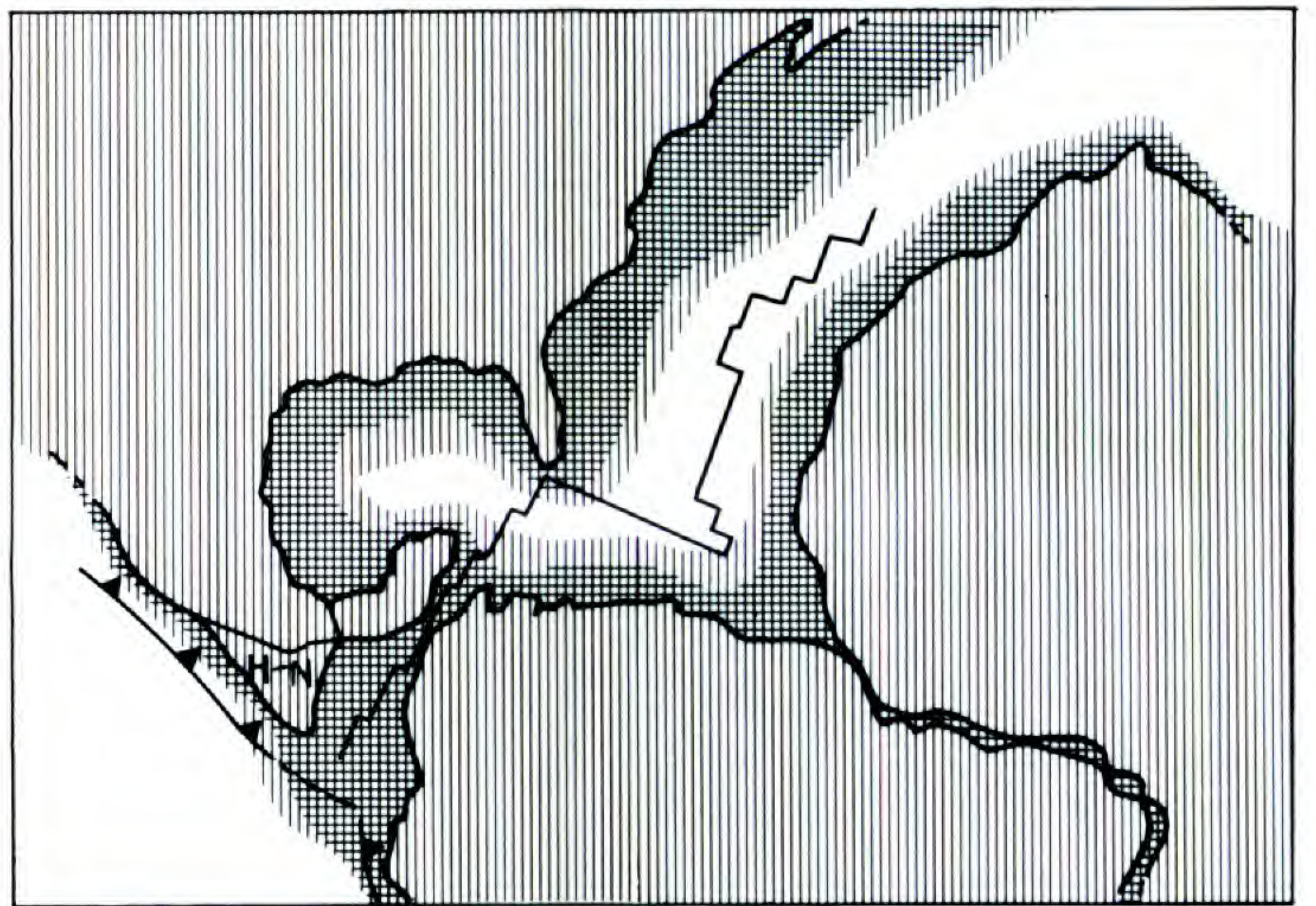


FIGURE 19. The Gulf of Mexico and Caribbean region in the Kimmeridgian (140 Ma) according to Pindell and Dewey (1982). The Yucatan block has rotated into position and been sutured to southern Mexico. Northern Central America (Honduras and Nicaragua, H-N) is depicted as already sutured to southwestern Mexico.

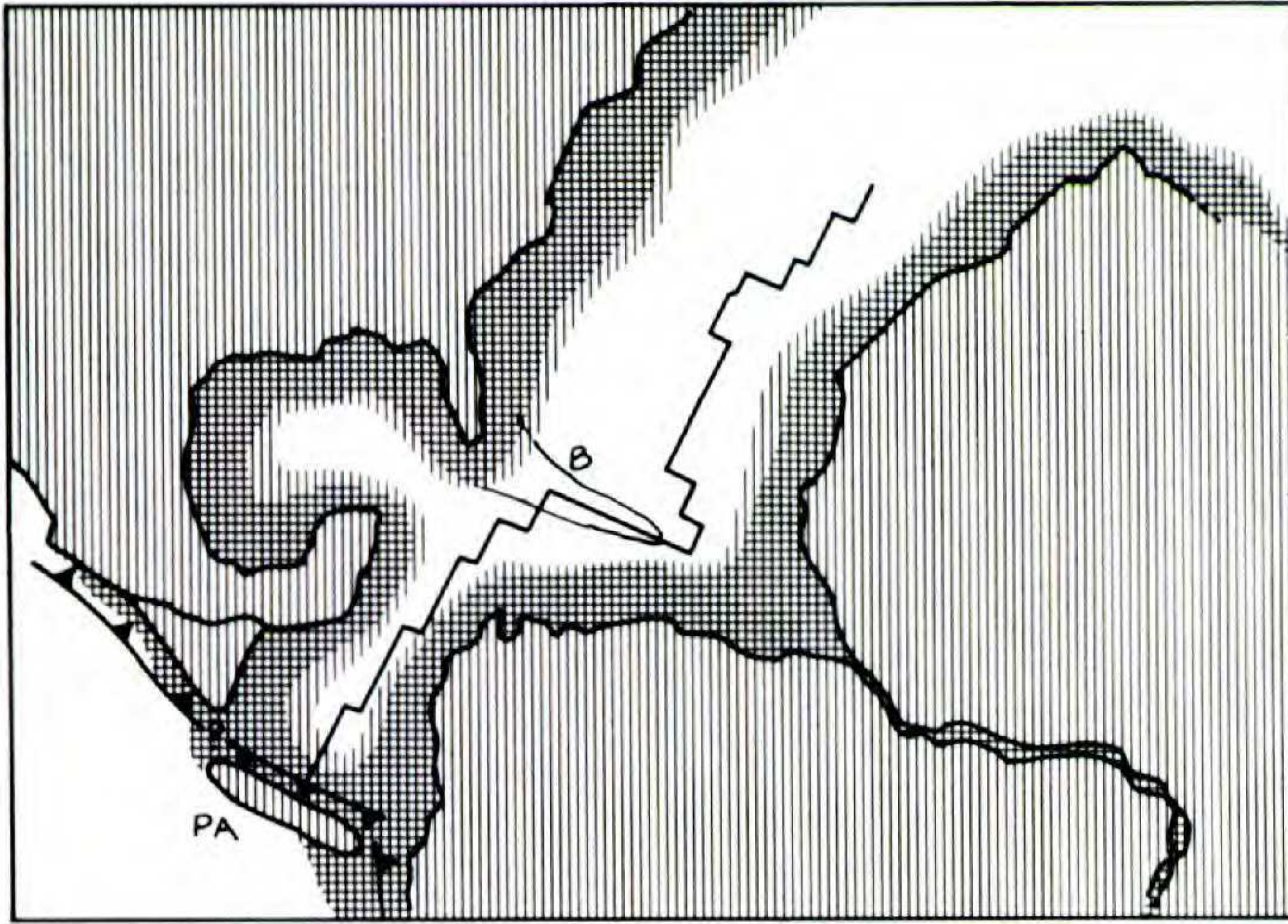


FIGURE 20. The Gulf of Mexico and Caribbean region at the time of formation of a proto-Antillean archipelago (PA) at 125 Ma, according to Pindell and Dewey (1982). The Bahama platform (B) can be seen extending in an ESE direction toward the proto-mid-Atlantic ridge.

water had a complex history of connections between different geographic features being made and then broken and then reformed in another configuration. The history includes eight events of fragmentation and seven of hybridization. This is summarized below in the series of included maps that show that vicariant opportunities for the biota are about as numerous as hybridization events that provide opportunities for mixing of biotas. The geology of Hispaniola provides perhaps the most dramatic example of these two aspects of geohistory since it is alleged to have had a history of prior connection with northern Central America (Yucatan), Cuba, Jamaica, the

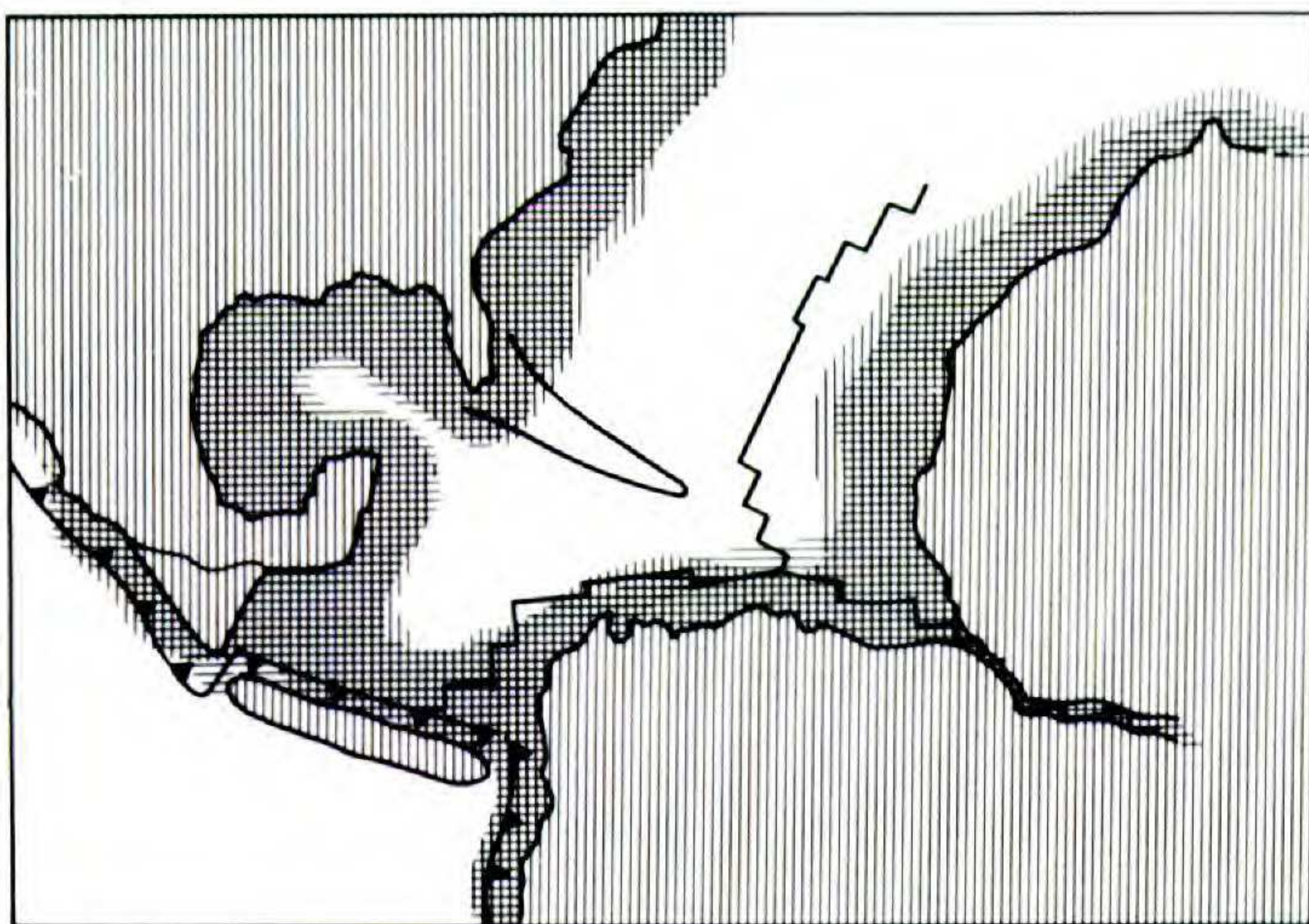


FIGURE 21. The Gulf of Mexico and the Caribbean region at the onset of separation of Africa and South America at 110 Ma, according to Pindell and Dewey (1982). The proto-Antillean archipelago has already moved slightly to the east of its position in the preceding figure.

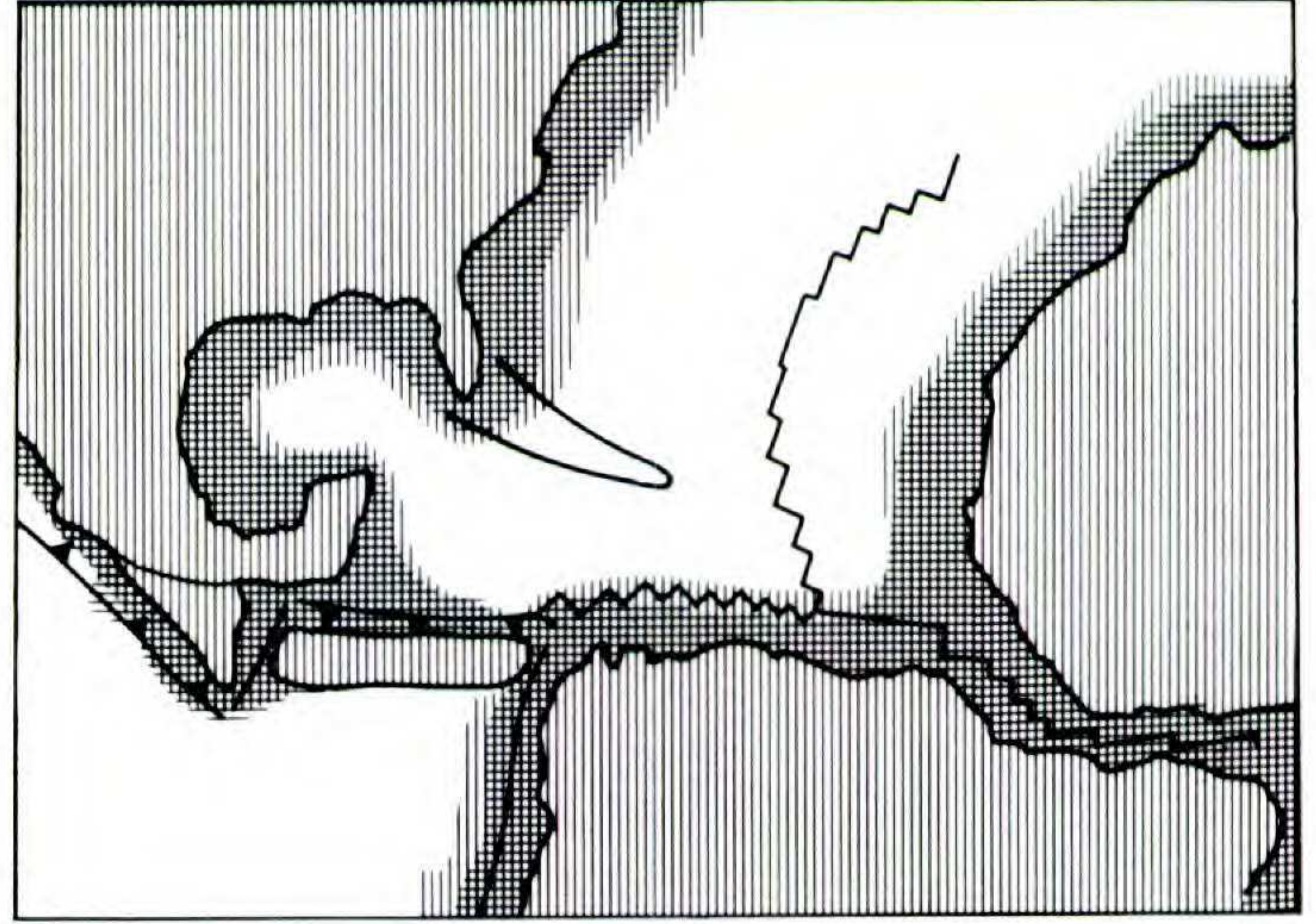


FIGURE 22. The Gulf of Mexico and the Caribbean region as eastern Pacific seafloor is initially being sucked into the Caribbean region at about 95 Ma, according to Pindell and Dewey (1982).

Bahamas and an early process of fragmentation from other proto-Antillean components into major segments that behaved independently for most of their reconstructed history. But perhaps the most interesting part of Caribbean geohistory is that involving the Chortis block and lower Central America, which appear to have been Pacific land accreted into the eastern margin of the Pacific borderlands, thus recalling some elements of the Pacifica concept of Nur and Ben-Avraham (1977). Another recent study has further documented the incorporation of allochthonous terranes into western North America (Minckley et al., in press). If part of the same phenomenon,

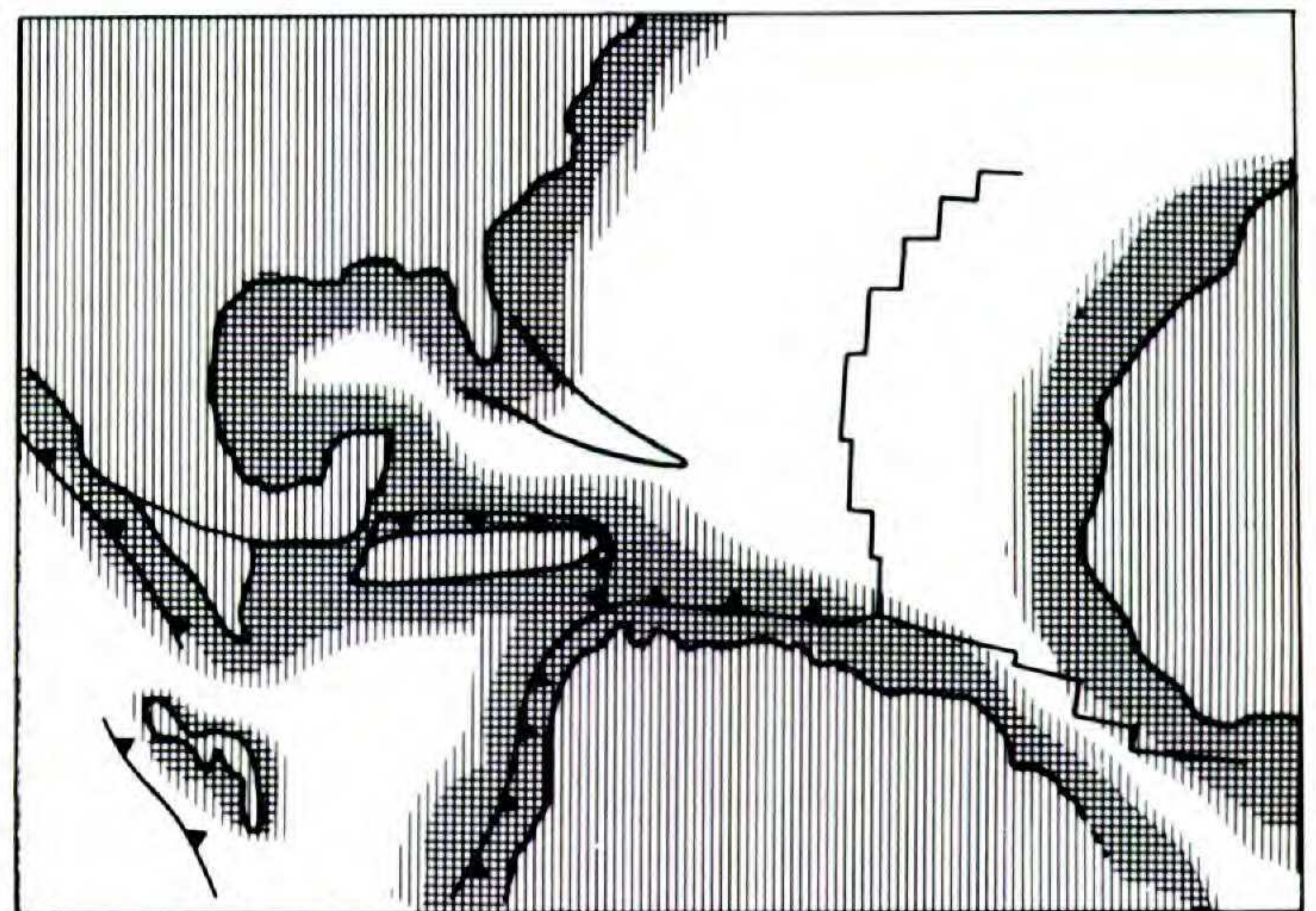


FIGURE 23. The Gulf of Mexico and the Caribbean region as the proto-Antillean archipelago at 80 Ma, according to Pindell and Dewey (1982), moves ENE toward the Bahama platform and a contact with the southeastern margin of the Yucatan. Note also the reconstruction of lower Central America as an eastern Pacific island arc near the western boundary of the Caribbean plate.

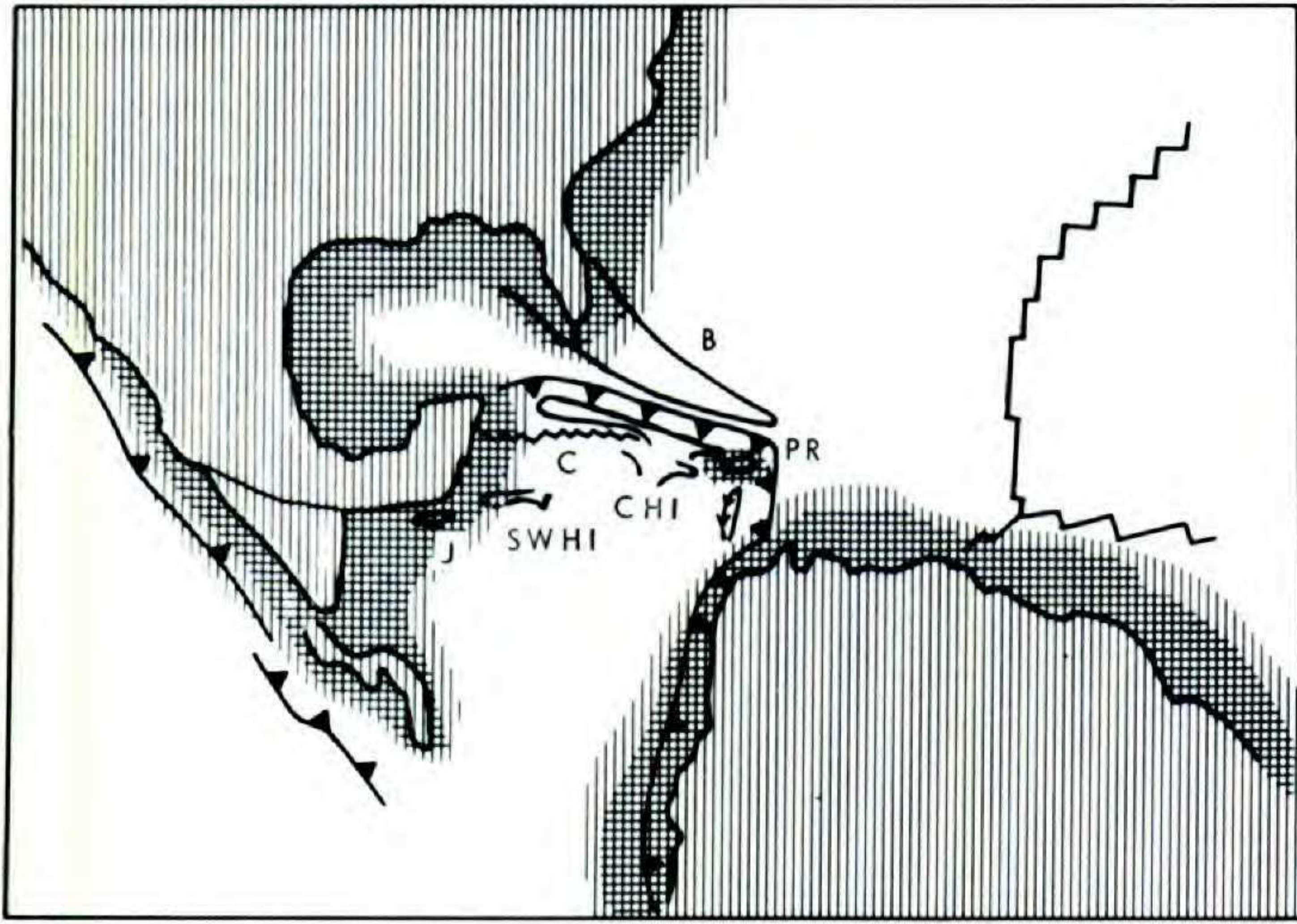


FIGURE 24. The Gulf of Mexico and the Caribbean region as the proto-Antillean archipelago begins to differentiate into recognizable components of the Greater Antilles at 65 Ma according to Pindell and Dewey (1982): Jamaica (J), central Hispaniola (SWHI), Puerto Rico (PR), and Cuba (C) that lies just north of the beginnings of the Cayman Trough (jagged line and CHI).

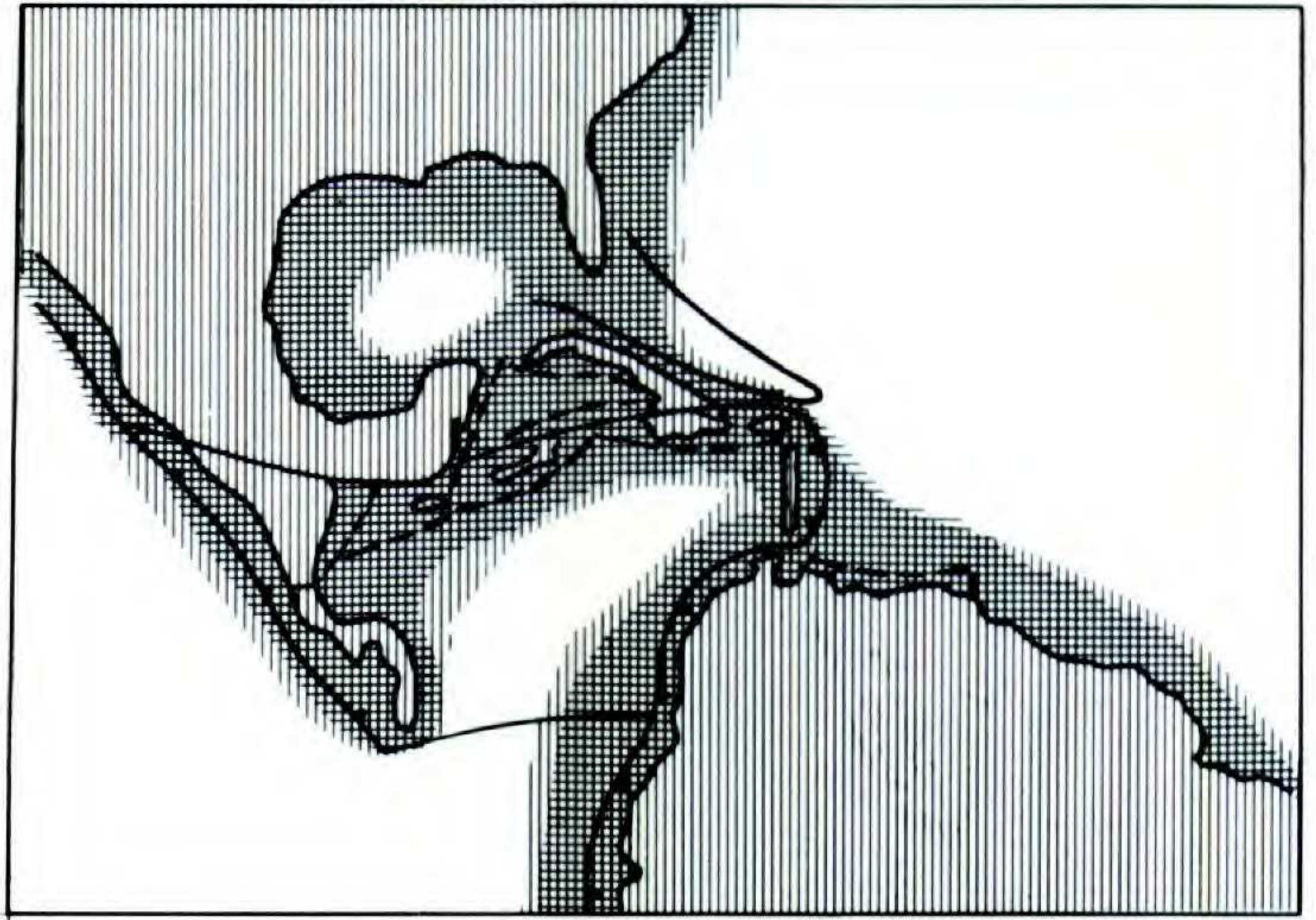


FIGURE 26. The Gulf of Mexico and the Caribbean region at about 36 Ma when many of the Antillean elements have been differentiated, the Cayman Trough has become active and northern Central America has begun its eastward motion along the Polochic-Motagua fault, and central Hispaniola is sutured to southwestern Cuba according to Pindell and Dewey (1982).

the history of Central America might well be shared with that of the exotic terranes along the western margins of North and South America, including perhaps the Carnegie Ridge system (the Galapagos and Cocos Islands) (see Rosen, 1976).

DERIVING GEOLOGICAL AREA CLADOGRAMS

With a history this complex it must be obvious that no simple branching diagram can exactly express all the implied relationships nor, because of hybridizations, is a completely resolved

branching diagram possible. It is, therefore, my conclusion that most profit is to be gained from isolating parts of Caribbean history that represent stages in the evolution of land and water and therefore stages during which today's complex biota can be understood. There is evidence from occurrences of endemic species that some major monophyletic groups have been around for a very long time, e.g., gars, synbranchid eels, land iguanas, decapod crustaceans, and probably also cichlid fishes (see Rosen, 1976). Regarding the West Indian butterfly fauna, Brown (1978) has written: "It is possible that the original fauna

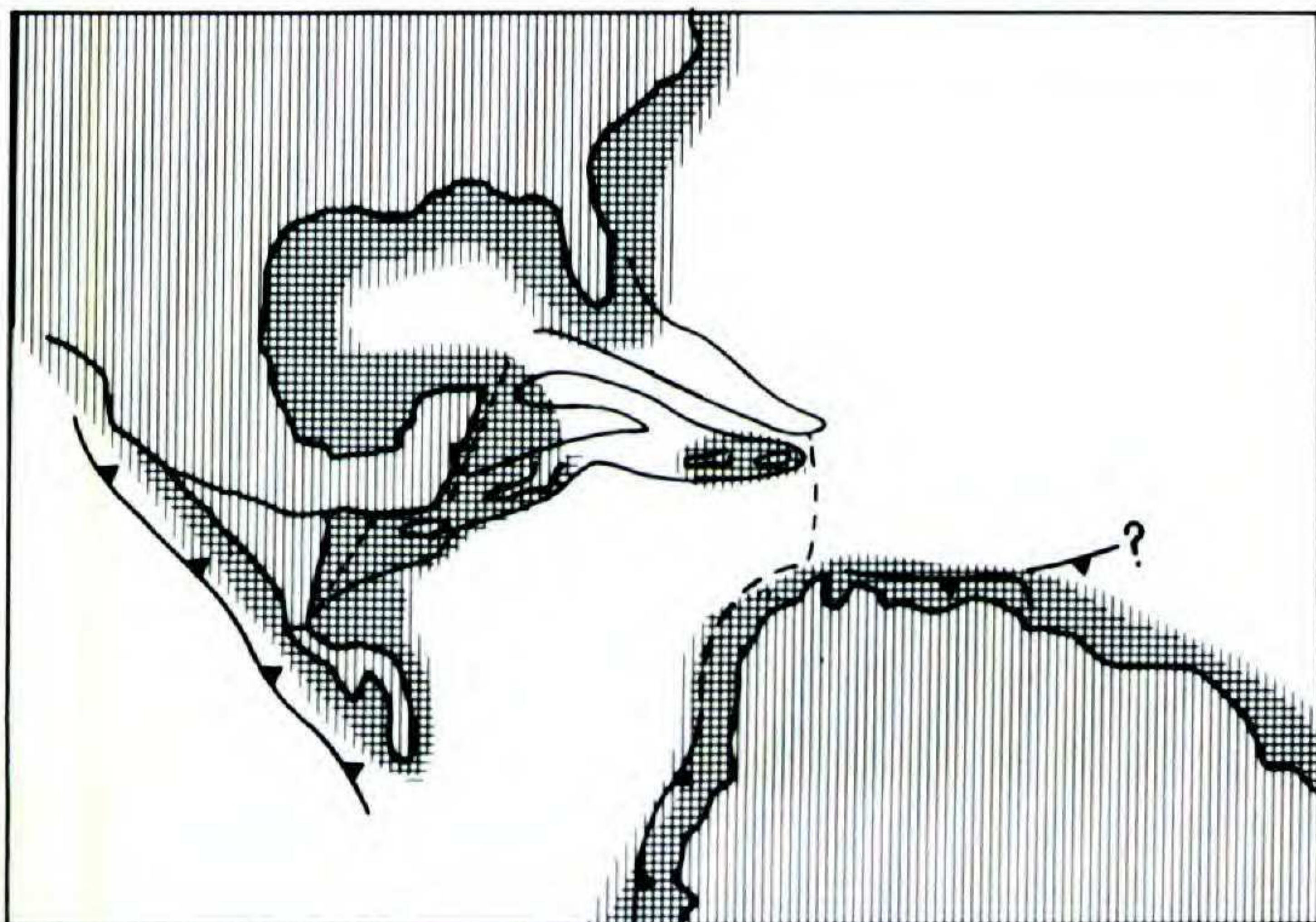


FIGURE 25. The Gulf of Mexico and the Caribbean region showing further differentiation of the Greater Antilles, the approximation of Cuba with the Bahama platform, and the suturing of lower Central America onto northern Central America at about 53 Ma according to Pindell and Dewey (1982).



FIGURE 27. The Gulf of Mexico and the Caribbean region at about 21 Ma when, according to Pindell and Dewey (1982), a spreading center has appeared in the Cayman Trough thus speeding the eastward movement of Jamaica, southwestern Hispaniola, and the disjunction of central Hispaniola and Cuba.

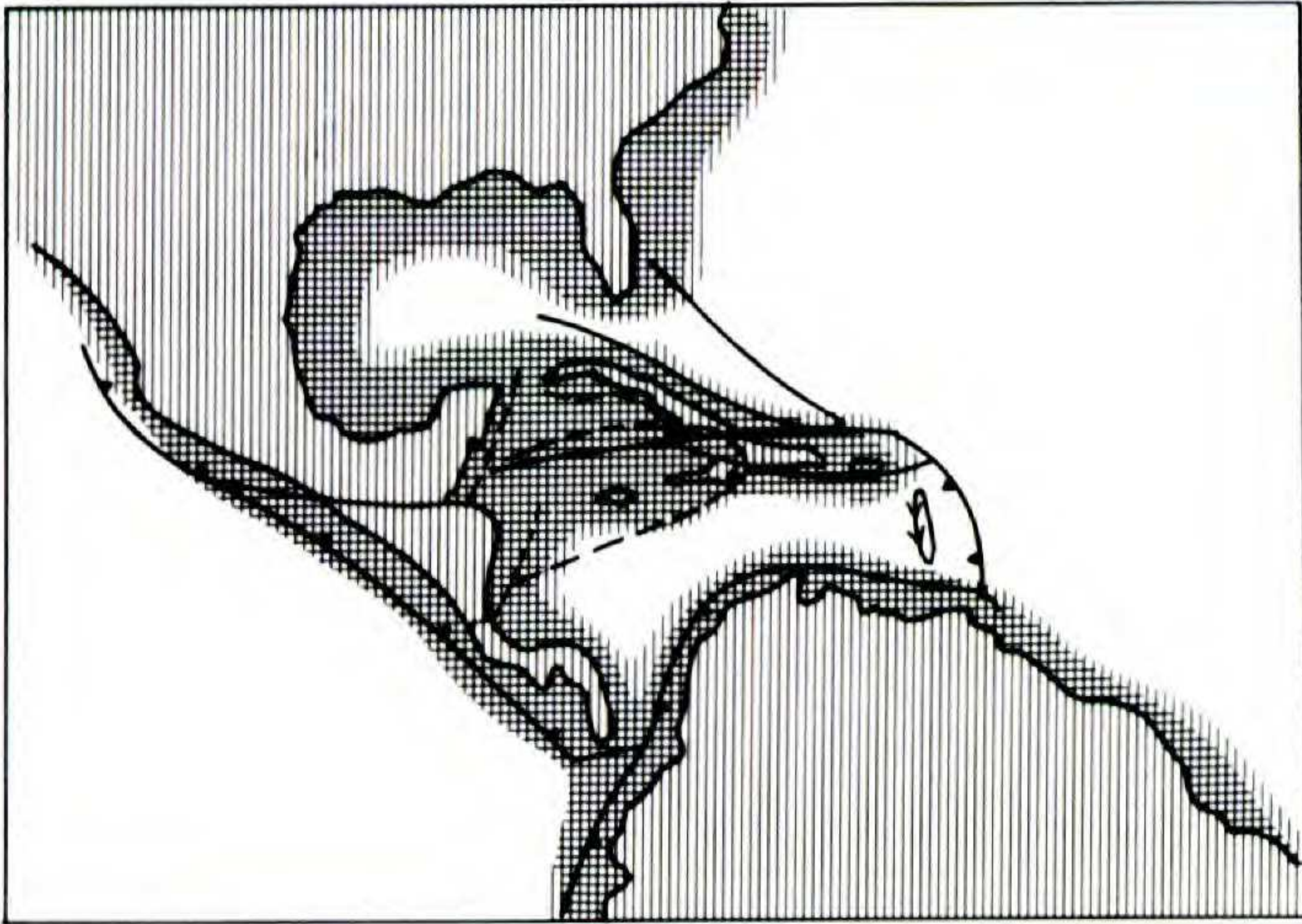


FIGURE 28. The Gulf of Mexico and the Caribbean region at about 10 Ma when, according to Pindell and Dewey (1982), Central America has made its closest approach to northwestern South America, Hispaniola is nearly assembled into its modern configuration and is almost disjunct from Cuba while making its closest approach to the southwestern tip of the Bahama platform.

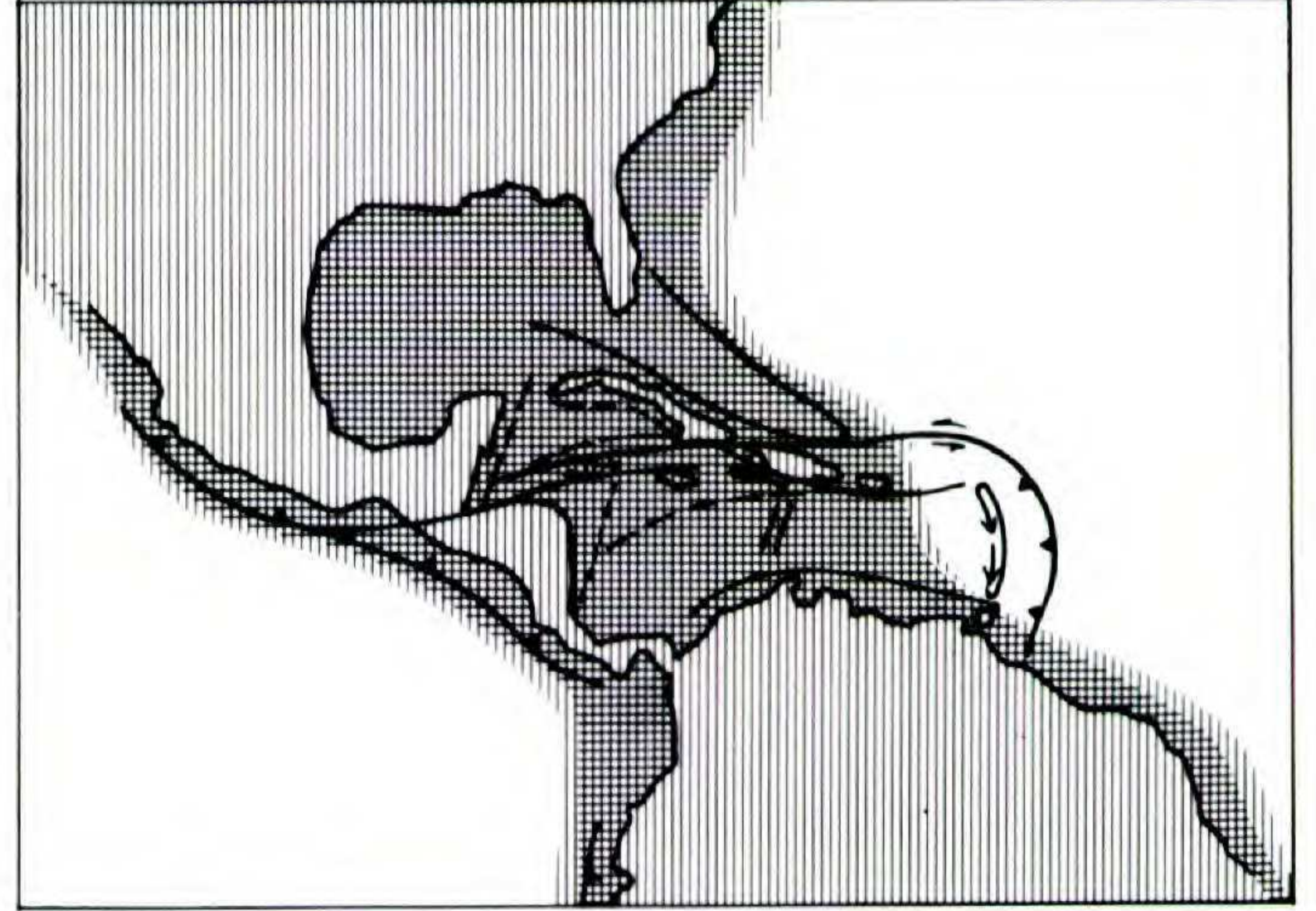


FIGURE 29. The Gulf of Mexico and present plate boundaries and land areas in the Caribbean region from Pindell and Dewey (1982).

of the region had its roots in Africa at the close of the Mesozoic Era. Very little of this fauna is left but there are some indications of it." Other taxa seem to reflect events in the less remote

periods of North and Middle American biohistory (Rosen, 1978). It would, therefore, be most helpful to be able to compare biological area cladograms with specific periods in geohistory rather than, as was done before (Rosen, 1976), to simply identify components the modern biota that are consilient with some features of today's complex geography. Thus one must introduce a

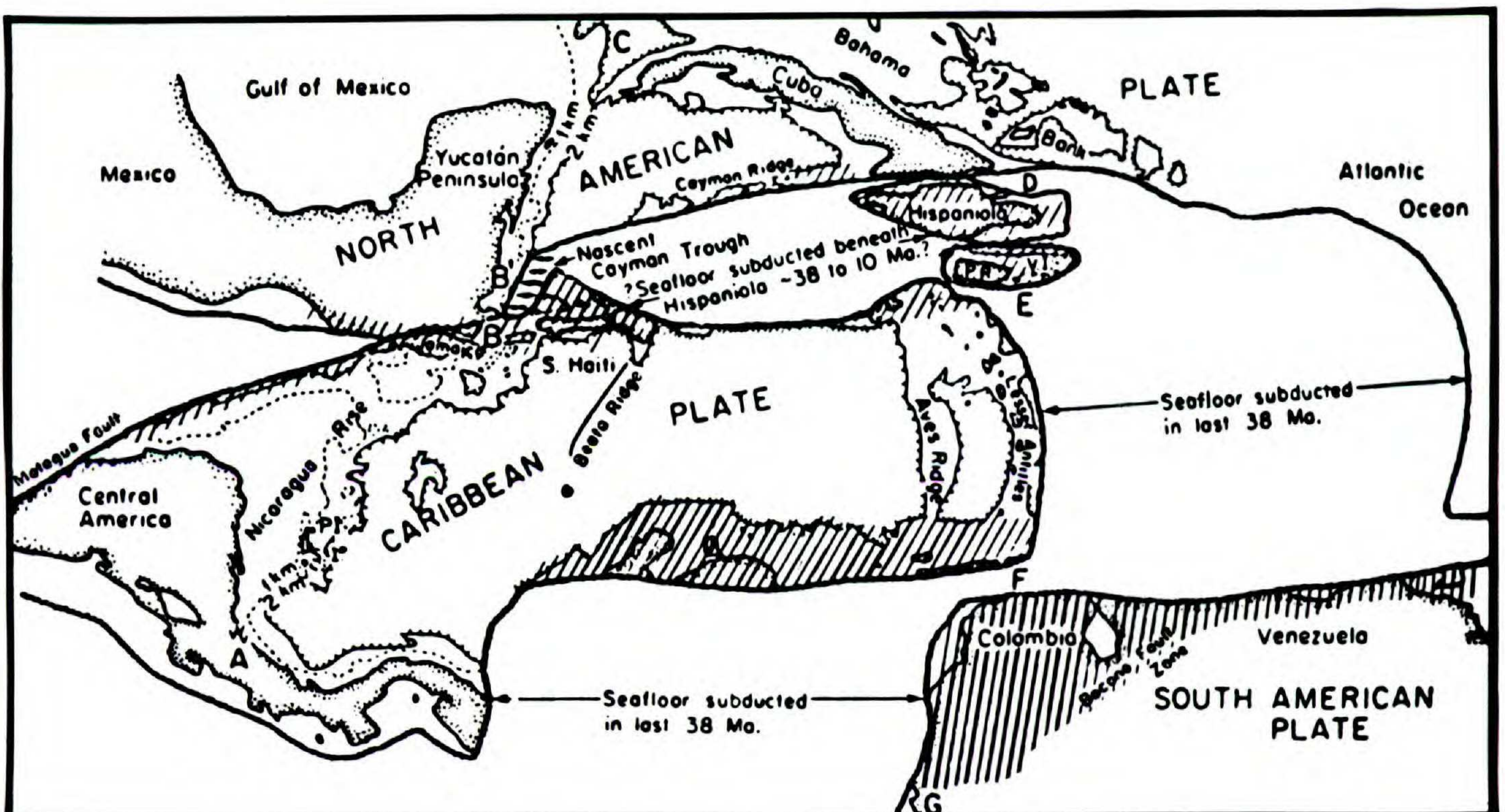


FIGURE 30. Caribbean microplate boundaries during the late Eocene (ca. 38 Ma) according to Sykes et al. (1982). In earlier Eocene times (ca. 48 Ma) Cuba, Hispaniola, and Jamaica are depicted as an archipelago extending from Yucatan toward northwestern South America (Fig. 31). In this reconstruction Puerto Rico is a neomorphic crustal feature that became subaerial late in Cenozoic history, but originally lay just south of the central Hispaniolan microplate and as in the Pindell and Dewey (1982) model. Hispaniola is complex incorporating a separate southwestern component and a small piece of the Bahamas to the north. Note that most of the main Antillean elements have, at most, a mid-Cenozoic age and that lower Central America was associated with the Chortis block by the early Miocene prior to an isthmian connection between North and South America.

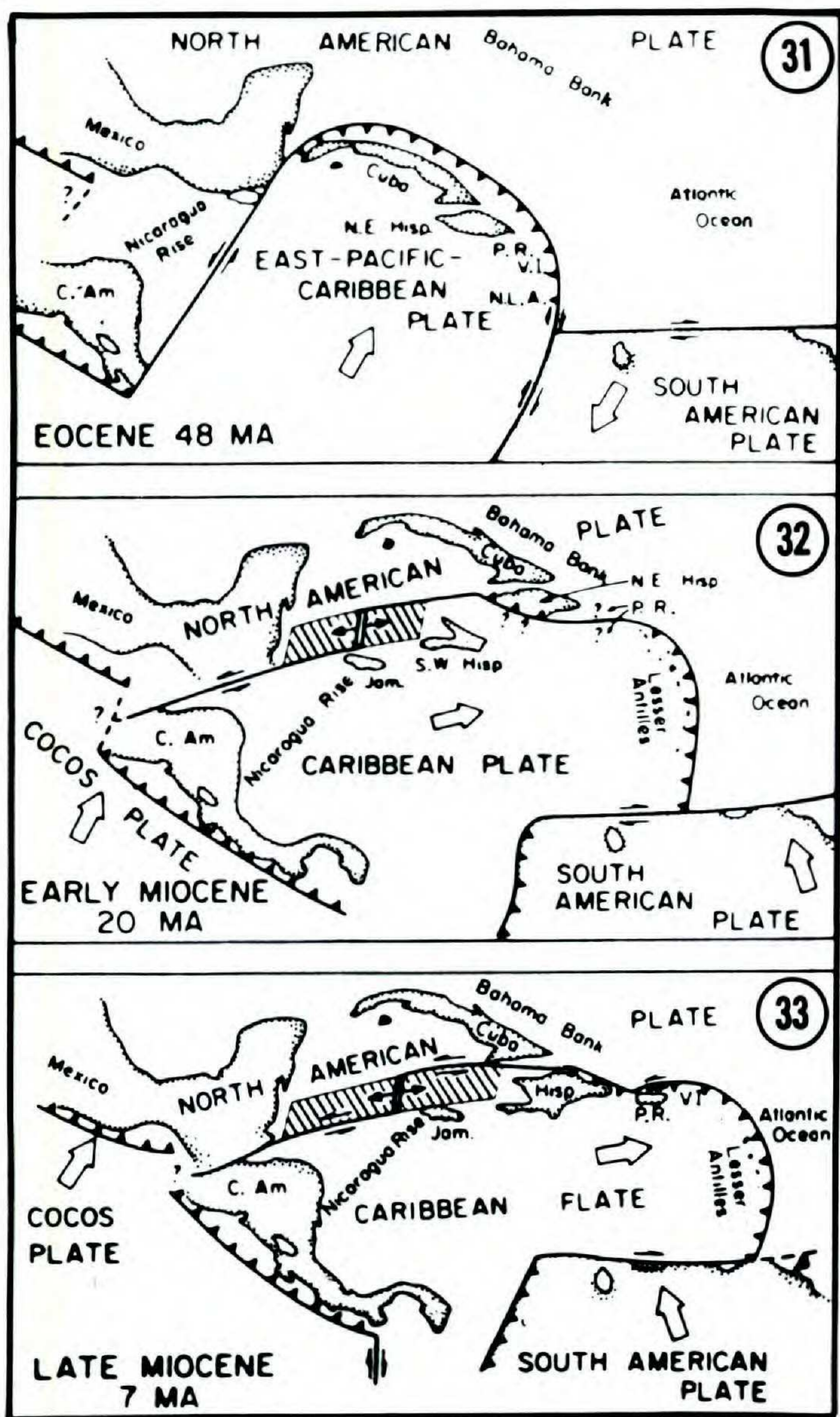


FIGURE 34. Eocene plate configuration (ca. 40 Ma) according to Dickinson and Coney (1980). A proto-Greater Antilles magmatic arc flips polarity of subduction to north facing as it transforms northeastward along the Yucatan escarpment and colliding with the Florida-Bahama bank where arc activity is extinguished.

CLADISTIC ANALYSIS

From the standpoint of Antillean history, the simplest place to begin is at that point 65 Ma when a proto-Antillean archipelago connected northern Central America (Yucatan) with northwestern South America (Figs. 33–44). This history can be divided into five components that will take us up to the modern period. In the earliest configuration (Fig. 33), the archipelago consists of 1) western Cuba and its sheared off fragments (Jamaica and southwestern Hispaniola) that are closely associated with northern Central America (Yucatan), and 2) eastern Cuba and its closely associated central Hispaniola. At this stage the Chortis block (Honduras-Nicaragua) is either Pacific land unconnected to northern Central America (Yucatan) or is sutured to western Mexico considerably to the north of the proto-Antillean archipelago.

Branching diagrams representing the complex history of the Caribbean must take into account both accretionary events, of which I identify seven since the main continental separation began about 165 Ma ago, and fragmentation events, of which I identify eight, including the initial continental separation.

Fragmentation events (roughly in order of decreasing age)

1. North America–Africa
2. North America–South America
3. Southern Mexico–North America

FIGURES 31–33.—31. The eastern Pacific and Caribbean in mid-Eocene times (ca. 48 Ma) according to Sykes et al. (1982). An intimate association between Jamaica, Cuba, and Hispaniola is depicted.—32. The Caribbean plate in early Miocene times (ca. 20 Ma), according to Sykes et al. (1982), showing the formation of a Cayman Trench spreading center on the site of the older Cayman Ridge, the continued association of central Hispaniola with eastern Cuba, and a now completed Chortis block/Isthmian Bridge.—33. The Caribbean in nearly its modern configuration in late Miocene times (ca. 7 Ma), according to Sykes et al. (1982), showing the still unconnected Isthmian Bridge with northwestern South America and the movement of Cuba eastward away from Yucatan. The Eocene age of this depiction is consistent with the age determinations of Wadge and Burke (1983) who also estimate a rate of plate motion of about 4 cm per year.

cladistic constraint so that explicit branching diagrams represent present areas of endemism that can be shown to be congruent with a branching diagram representing a specific part of Caribbean geohistory. The branching sequence must also agree with the time constraints (relative times) of accretion and fragmentation.

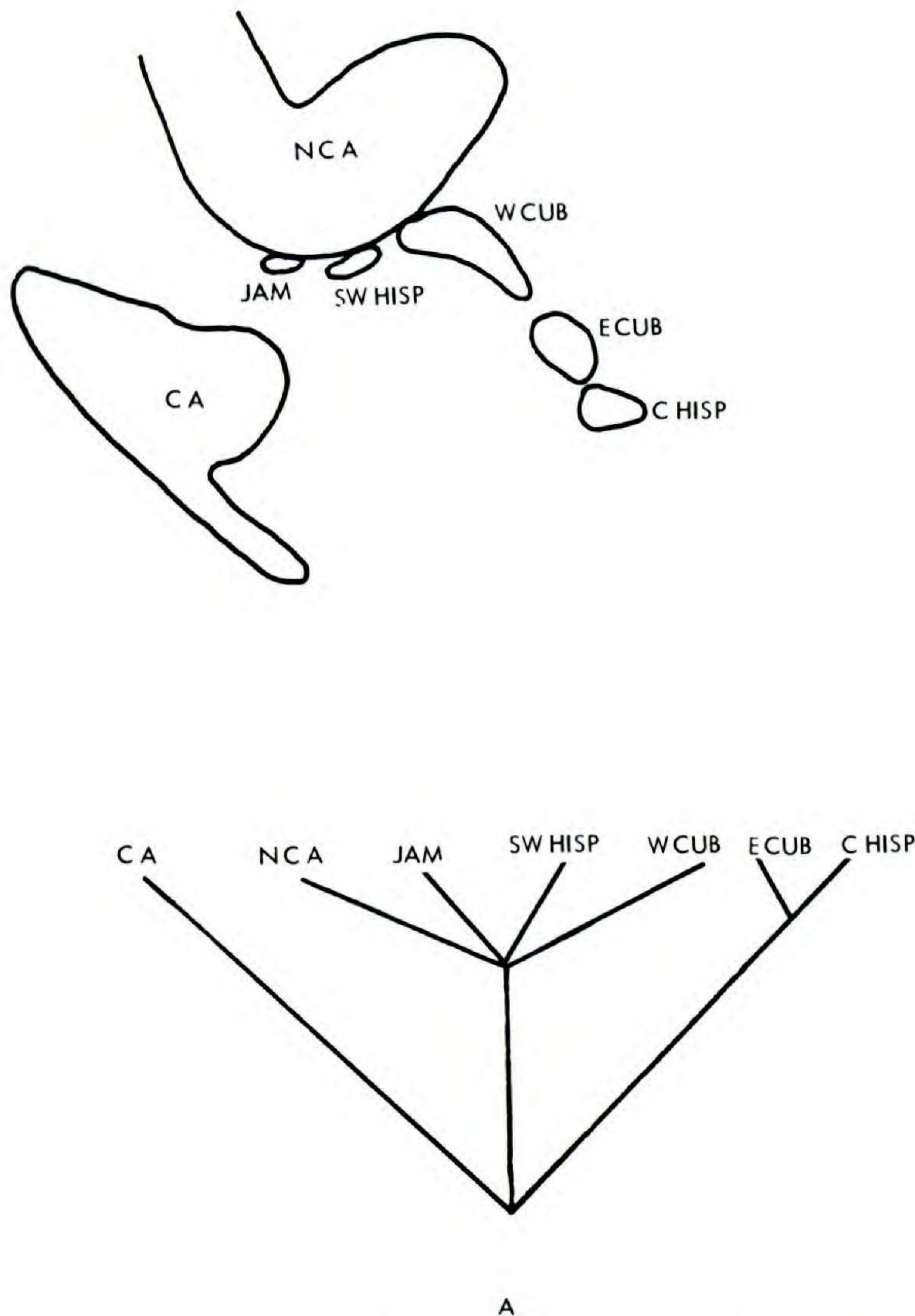


FIGURE 35. A diagrammatic consensus map of the mid-Cenozoic relations among some main components of the Caribbean heartland and a branching diagram that summarizes these relations.

4. South America–Africa
5. Southern Mexico (Yucatan)–western Cuba, Jamaica, southwestern Hispaniola
6. Eastern Cuba–Bahamas
7. Eastern Cuba–central Hispaniola
8. Hispaniolan Bahamas (fragment)–southern Bahamas

Accretionary events (roughly in order of decreasing age)

1. Yucatan–western Cuba, Jamaica, southwestern Hispaniola
2. Honduras, Nicaragua (?northern Costa Rica)–western to southwestern Mexico, and eventually to northern Central America (Yucatan)
3. Western Cuba–eastern Cuba
4. Eastern Cuba–central Hispaniola
5. Central Hispaniola–southwestern Hispaniola
6. Southern Bahamas (fragment)–central Hispaniola

7. Southeastern Costa Rica, Panama–northern Central America (Yucatan), northwestern South America

For the accretionary events there is an alternative model, differing in details of island sequence, and that is the one proposed by Carey (1958), recently discussed and illustrated by Nagel (1971, fig. 15) in which, in sequence from north to south, Jamaica, Puerto Rico, Hispaniola, and Cuba were a part of southern Mexico prior to their translation and rotation to a more easterly position. In this model the Bahamas lay between the tip of Florida and northern South America with an unspecified amount of intervening land, and Honduras-Nicaragua (the Chortis block), and the Yucatan (labelled Guatemala in Nagel's figure) were narrowly joined and both a part of the North American gulf coast. Also, in this model, it was the Lesser Antilles that formed an island arc connecting Mexico with South America in the early Mesozoic. From the standpoint of its relation to biogeography even this seemingly inverted model of land-area relationships yields the same general expectation of the biological relationships of the Caribbean subregions. The general features of the relation between Caribbean tectonics and biogeography were discussed most recently by Durham (1985), but primarily in connection with the model proposed by Sykes et al. (1982). If we adopt the position that land areas formed of mutually exotic terranes through accretion, might exhibit taxic area relationships when later fragmented, a consequential inference is that accretionary events might be followed by biotic transfer across the suture zone prior to secondary fragmentation and the differentiation of the now isolated ancestral population and its transferred descendants. If so, geological area cladograms used for comparison with biological area cladograms must incorporate both accreted and fragmented areas.

Since a suture zone might serve to isolate original and transferred biotic elements because of increasing geographic disruption during the later phases of suturing, my geologic area cladograms adopt the potentially most informative interpretation by incorporating sutured areas (that have not secondarily fragmented) on an equal basis with those that have secondarily separated.

Nevertheless, in a general cladogram of areas based on both fragmentation and accretion, land hybridizations would be represented either as reticulations (lines joining two or more branches)

or, as in the case of biological hybridizations, as unresolved branches representing the parent taxa and the hybrid. This is the conservative procedure adopted here. One might suppose that land hybridization (e.g., the Chortis block with southern Mexico, eastern with western Cuba, and eastern Cuba with central Hispaniola) would lead to a sharing of biotas by the joined fragments, but that supposition requires the subsidiary idea, probably correct in some instances but not others, that the suture zone presents no obstacle to biotic mixing. At least some suture zones seem perfectly hospitable to organisms, as in the case of the Chortis block suture zone (referred to as the Polochic-Motagua transform fault) where persistent, small-scale seismic activity, and the formation of a major down-dropped block of land (e.g., Lago Isabal) have not been inimical to the survival of faunal elements within the region [e.g., the poeciliid fishes discussed by Rosen (1979) and their occurrence on both sides of the Motagua-Polochic synclinal depression]. Other organisms, such as the swamp eels of the genera *Ophisternon* and *Synbranchus*, seem unusually sensitive to this fault line (see Rosen & Greenwood, 1975), although species of *Ophisternon* occur in the Yucatan and in Cuba, indicating that distributional boundaries cannot be assumed from geological data.

Even though one can identify at least 16 geographic areas involving Caribbean history (if the continental regions are included), I have chosen only eight of these to illustrate a method whereby geological data might be presented for comparison with biological data. The chief objective is to be able to relate a given biological distribution pattern to a specified period in Caribbean geohistory.

A geological area cladogram representing these relationships can be written as shown in Figures 35–43. The first cladogram (Fig. 35) is unresolved with respect to four areas [northern Central America (Yucatan), Jamaica, southwestern Hispaniola, western Cuba]. To make the most convincing case we will take the most conservative stance and derive from this general cladogram all possible completely resolved four-taxon statements, of which there are six shown in Figure 36. Many more three-taxon statements are derivable, but three-taxon statements have the disadvantage of representing relatively trivial statements of relationship and therefore requiring much more comparative data to demonstrate general congruence. For example, for three-area

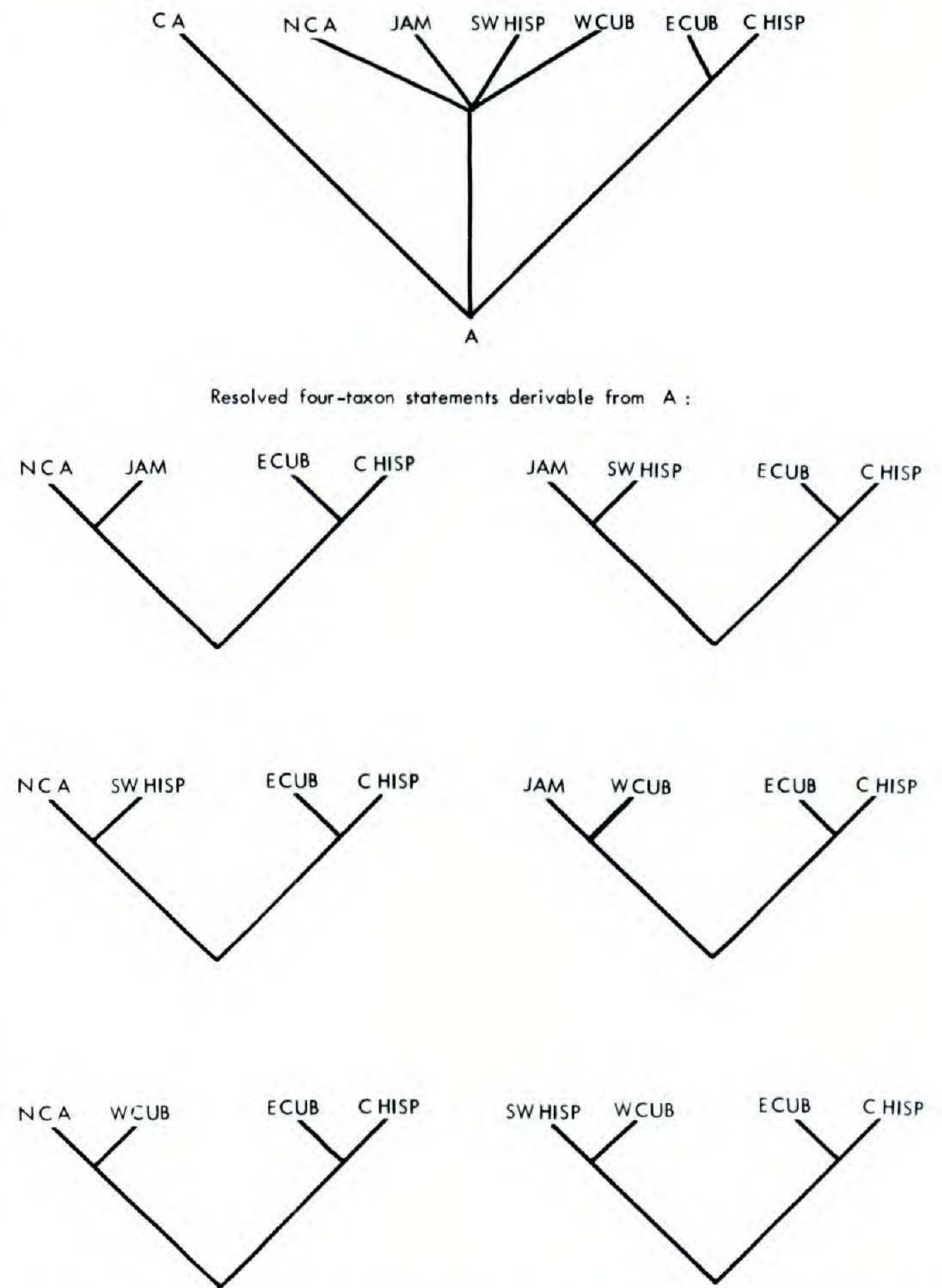
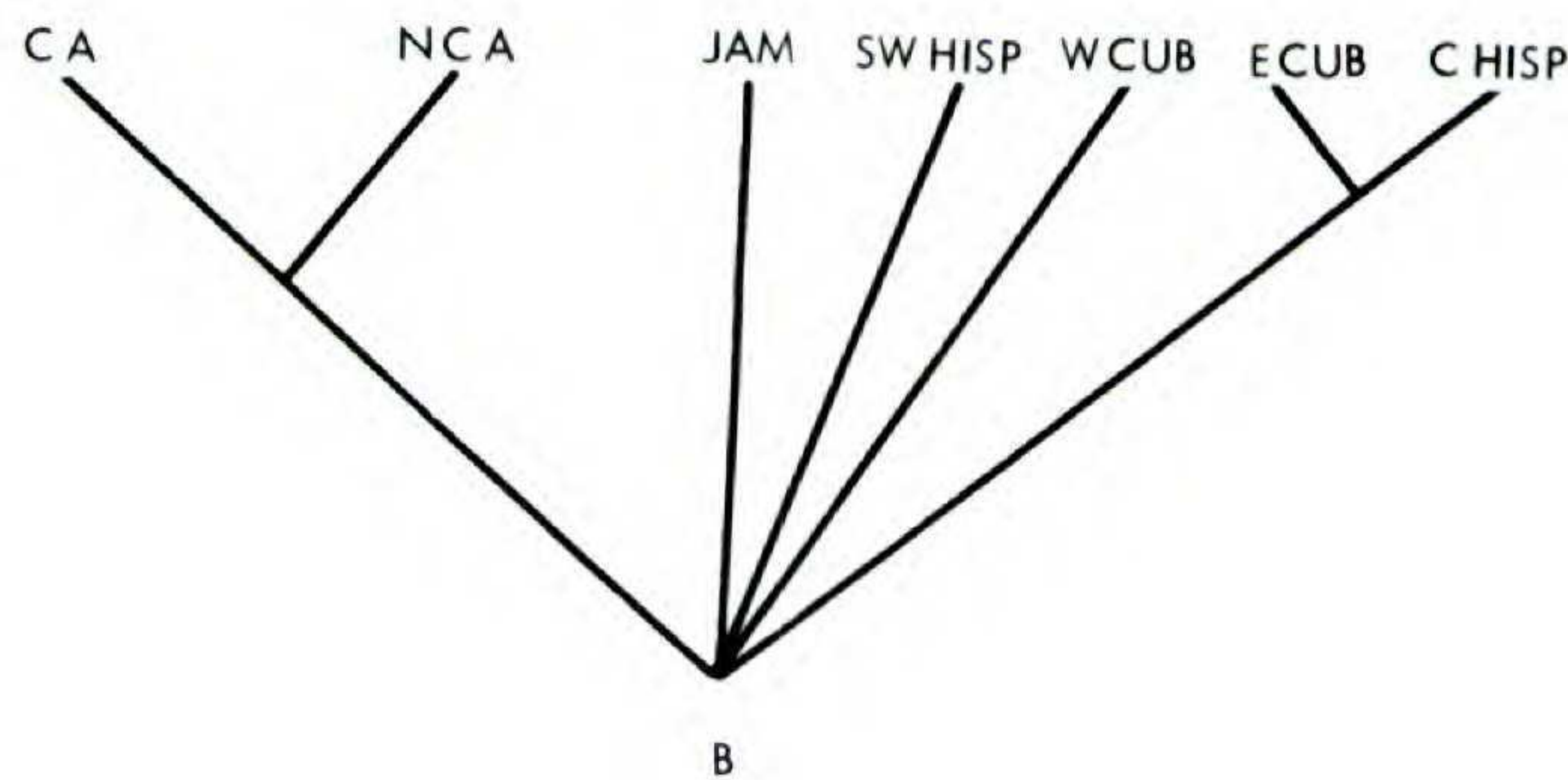
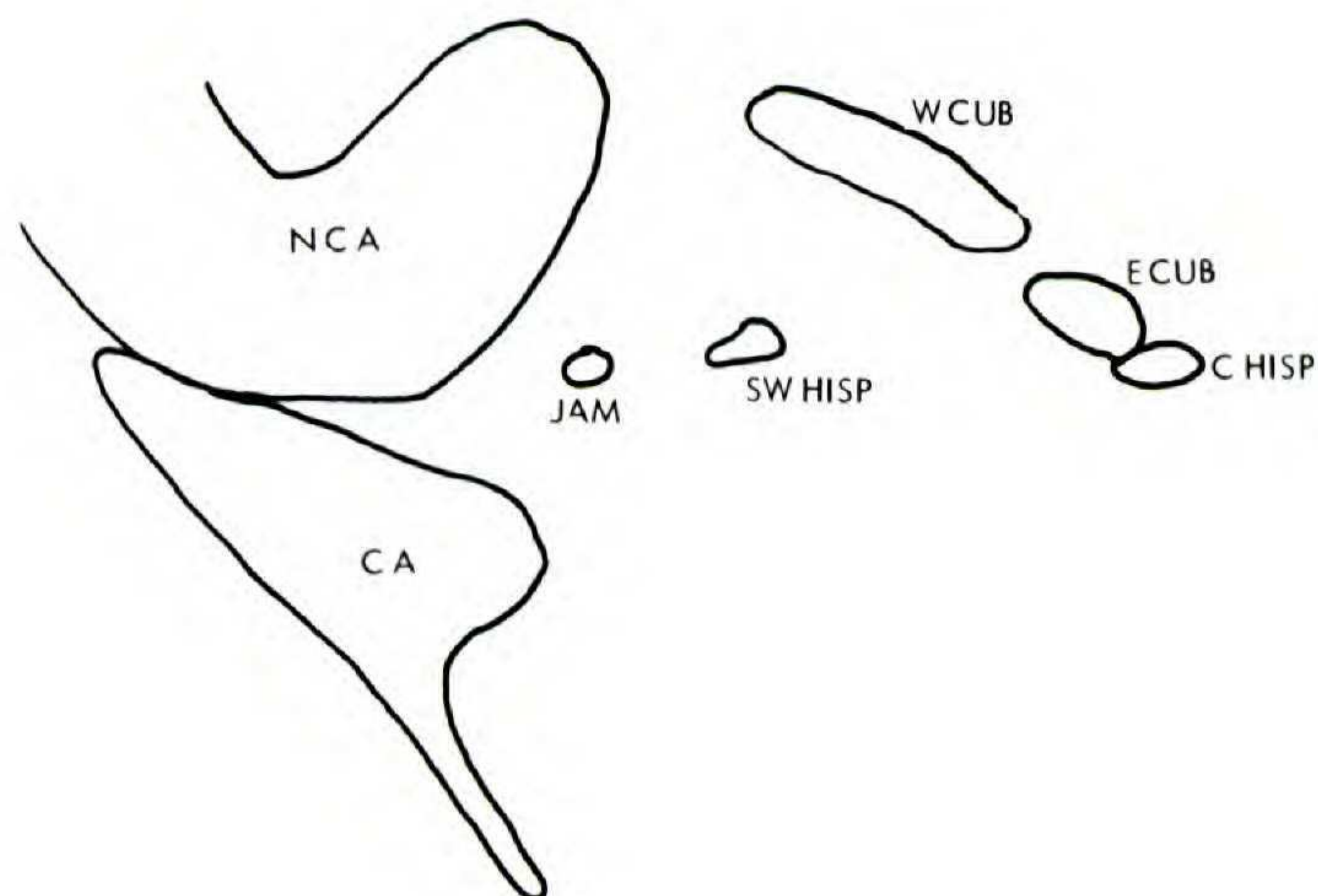


FIGURE 36. The branching diagram as in Figure 35 and the six completely resolved four-taxon, four-area statements derivable from it: CA, the Chortis block (southern Guatemala, Honduras, and Nicaragua); NCA, northern Central America (Yucatan); JAM, Jamaica; SWHISP, southwestern Hispaniola; WCUB, western Cuba; ECUB, eastern Cuba; CHISP, central or nuclear Hispaniola.

relationships there are only three possible solutions: A-B-C, A-C-B, B-A-C and two replications of one of these patterns would yield a probability that the congruence was ruled by chance once in every 27 trials ($3 \times 3 \times 3$), whereas there are 15 possible solutions to a four-taxon system (Nelson & Platnick, 1981; Rosen, 1978) and two replications of a given pattern would yield a probability of once in every 225 trials ($15 \times 15 \times 15$) that the congruence was random.

In the next geographic configuration in which the proto-Antillean archipelago begins to move eastward into the Caribbean region some of the earlier relationships are maintained (western Cuba, Jamaica, southwestern Hispaniola) and others are broken (western Cuba, Jamaica, southwestern Hispaniola) and a new association is established (the Chortis block with northern Central America). The general cladogram (Fig. 37) representing these relationships includes one land hybridization and three vicariant events and



Resolved four-taxon statements derivable from B :

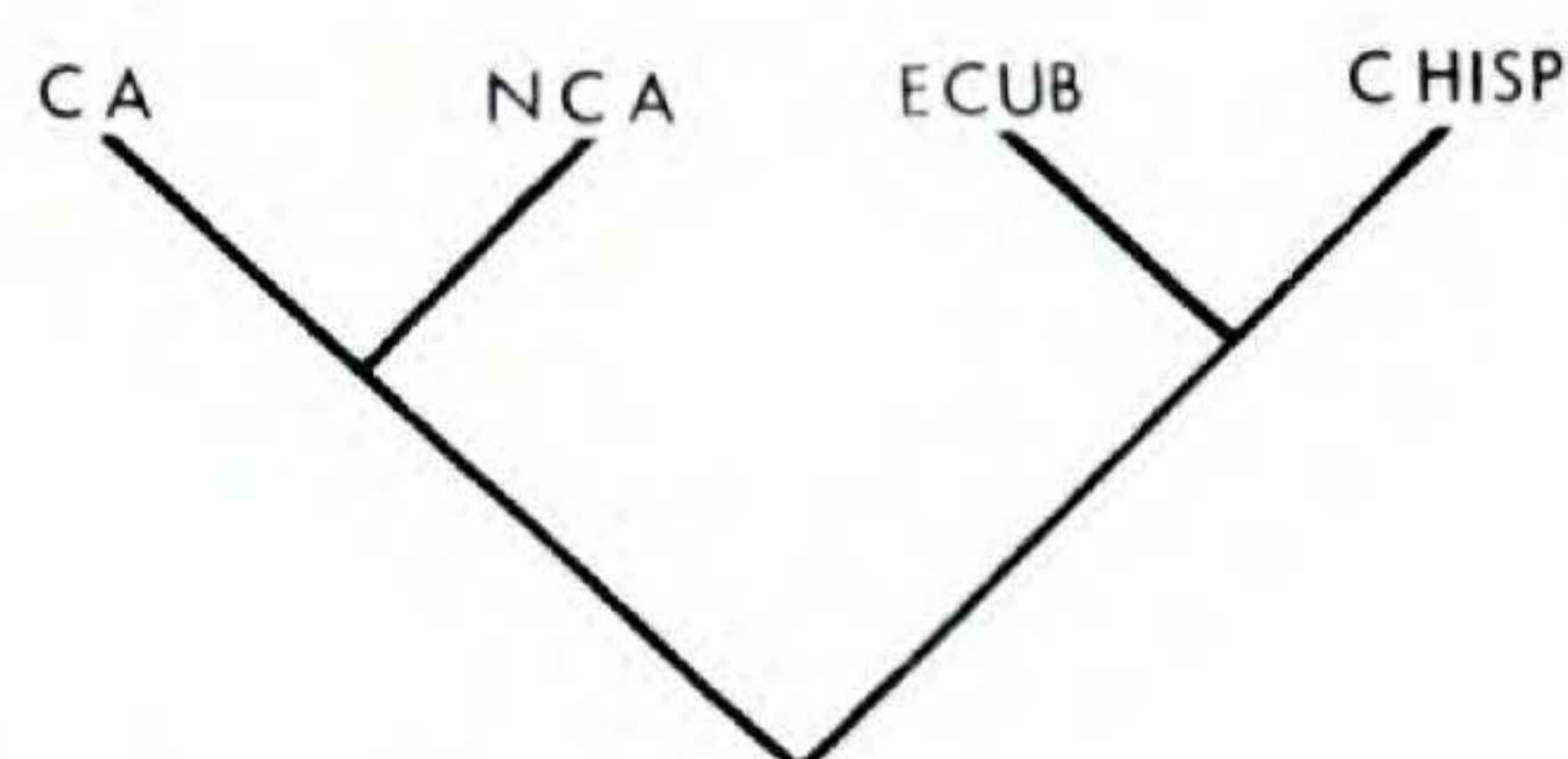
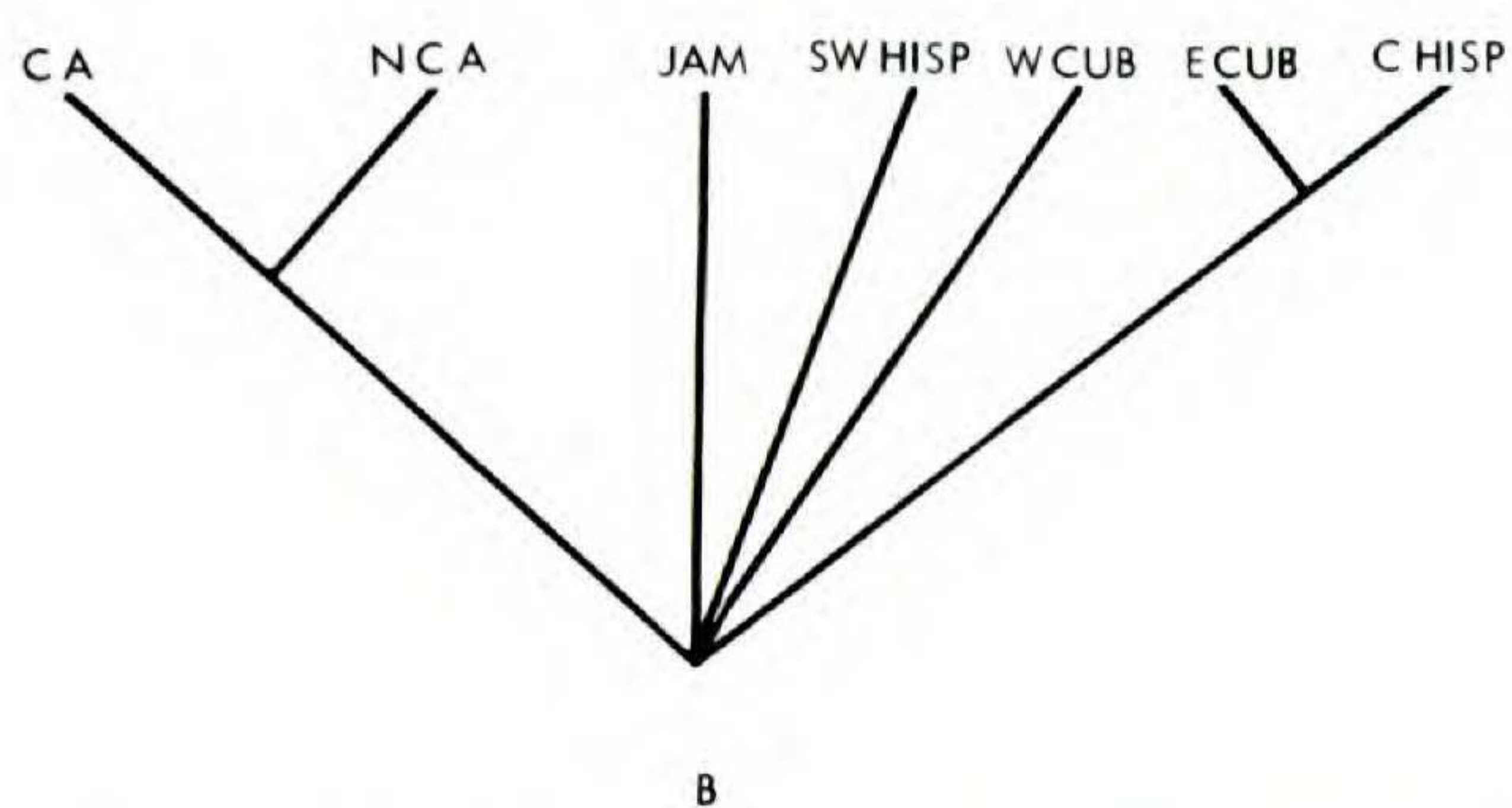


FIGURE 38. The branching diagram as in Figure 37 and the single, completely resolved four-taxon, four-area statement derived from it: abbreviations as in Figure 36.

FIGURE 37. A diagrammatic consensus map of the late Eocene relations among some main components of the Caribbean heartland and the branching diagram that summarizes these relations.

includes a pentachotomy. From this general statement only a single resolved four-taxon statement is derivable (Fig. 38).

As eastward movement of the Antilles continues, central Hispaniola separates from eastern Cuba but western Cuba and eastern Cuba are joined (Fig. 39). This general cladogram also includes a tetrachotomy from which may be derived but a single resolved four-taxon statement (Fig. 40). Continued movement of the Caribbean plate brings southwestern Hispaniola and central Hispaniola into contact and, although no new mainland relationships are being established, the Chortis block continues to slide eastward against northern Central America (Yucatan) on the Motagua-Polochic fault so that at least new contiguous land-area-relationships are being established (Fig. 41). Here, too, the general cladogram includes a pentachotomy but gives rise to three resolved four-area cladograms (Fig. 42). In the modern configuration a new land contact is established between southern Bahamas and His-

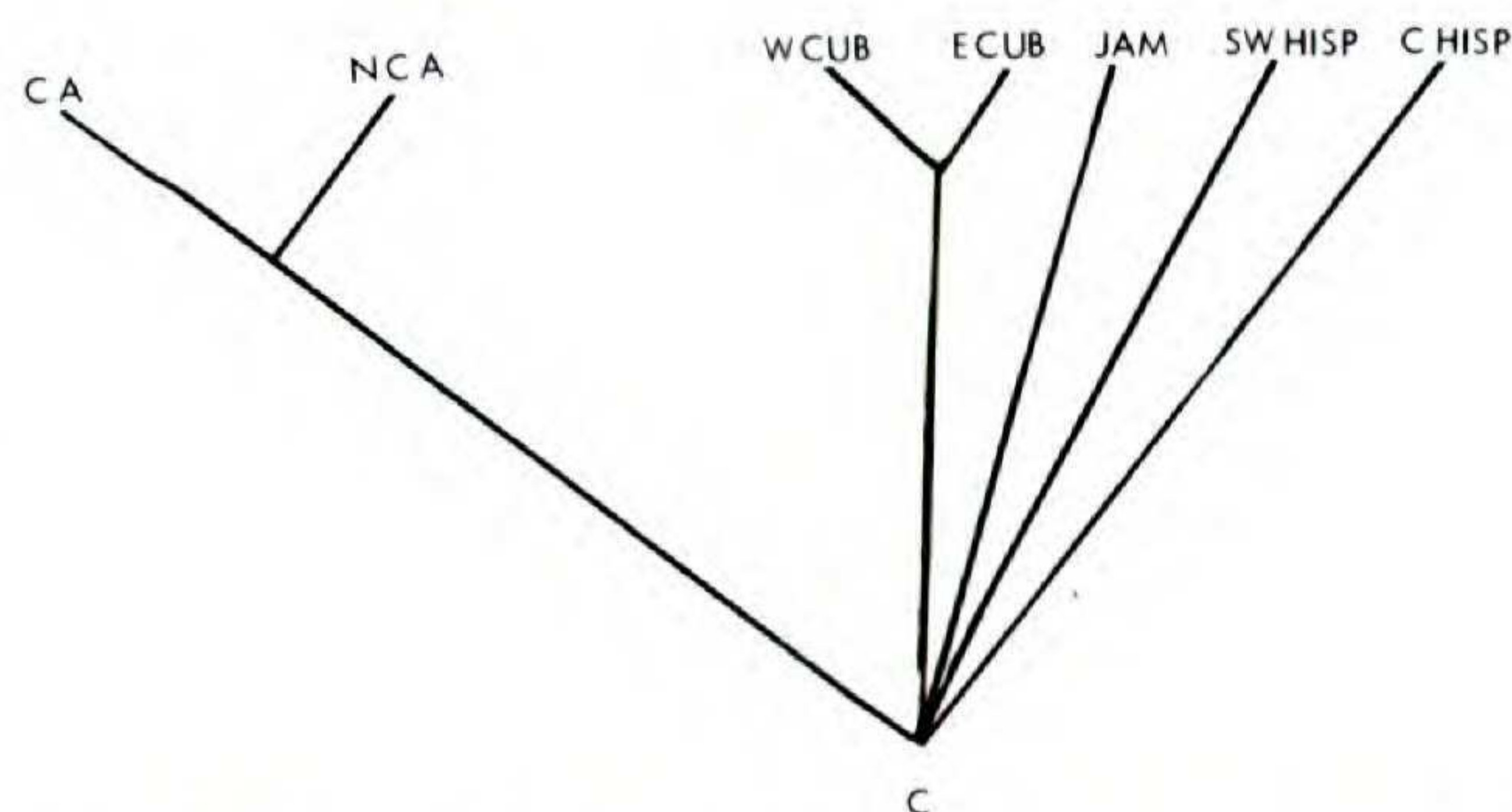
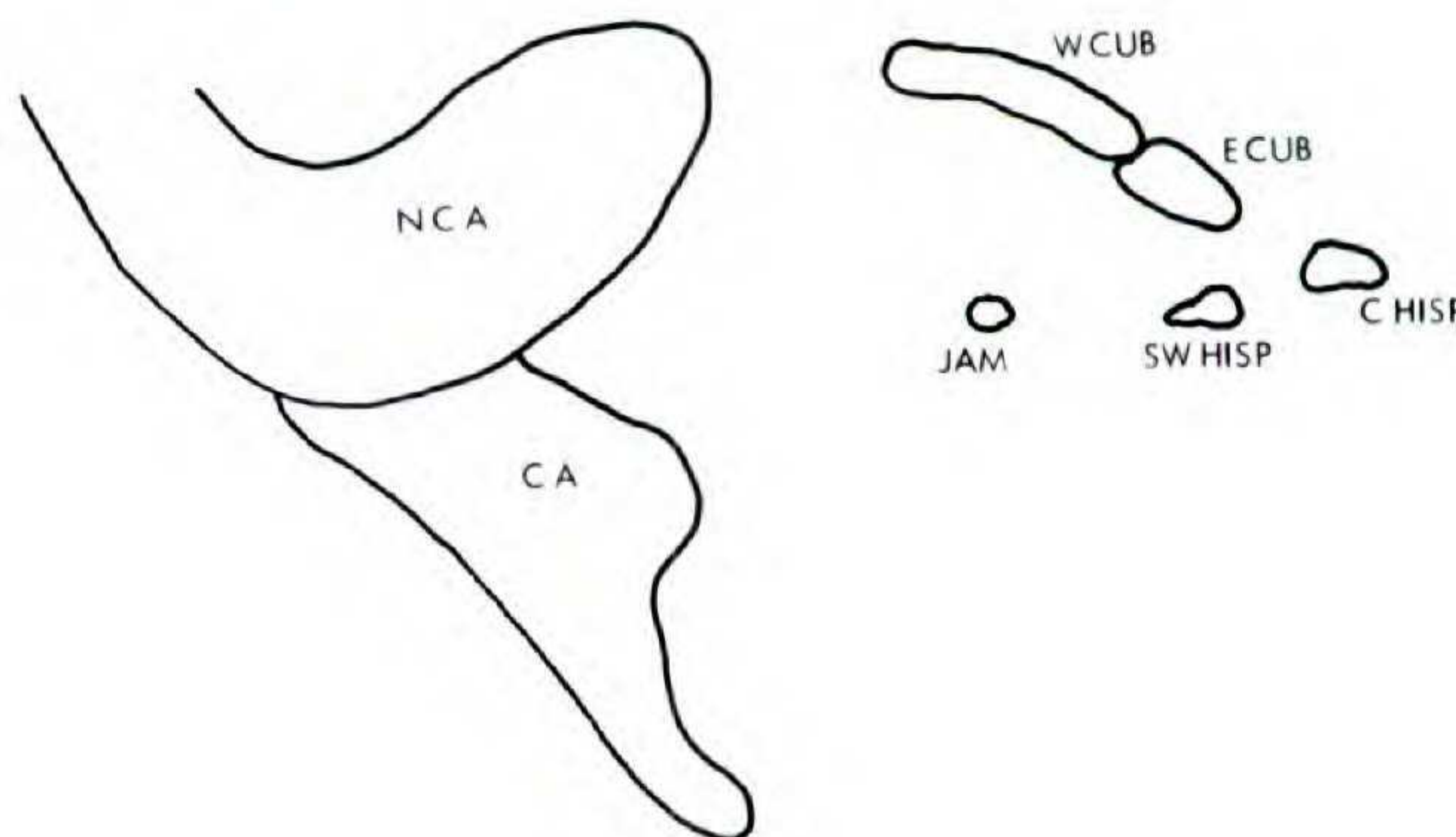
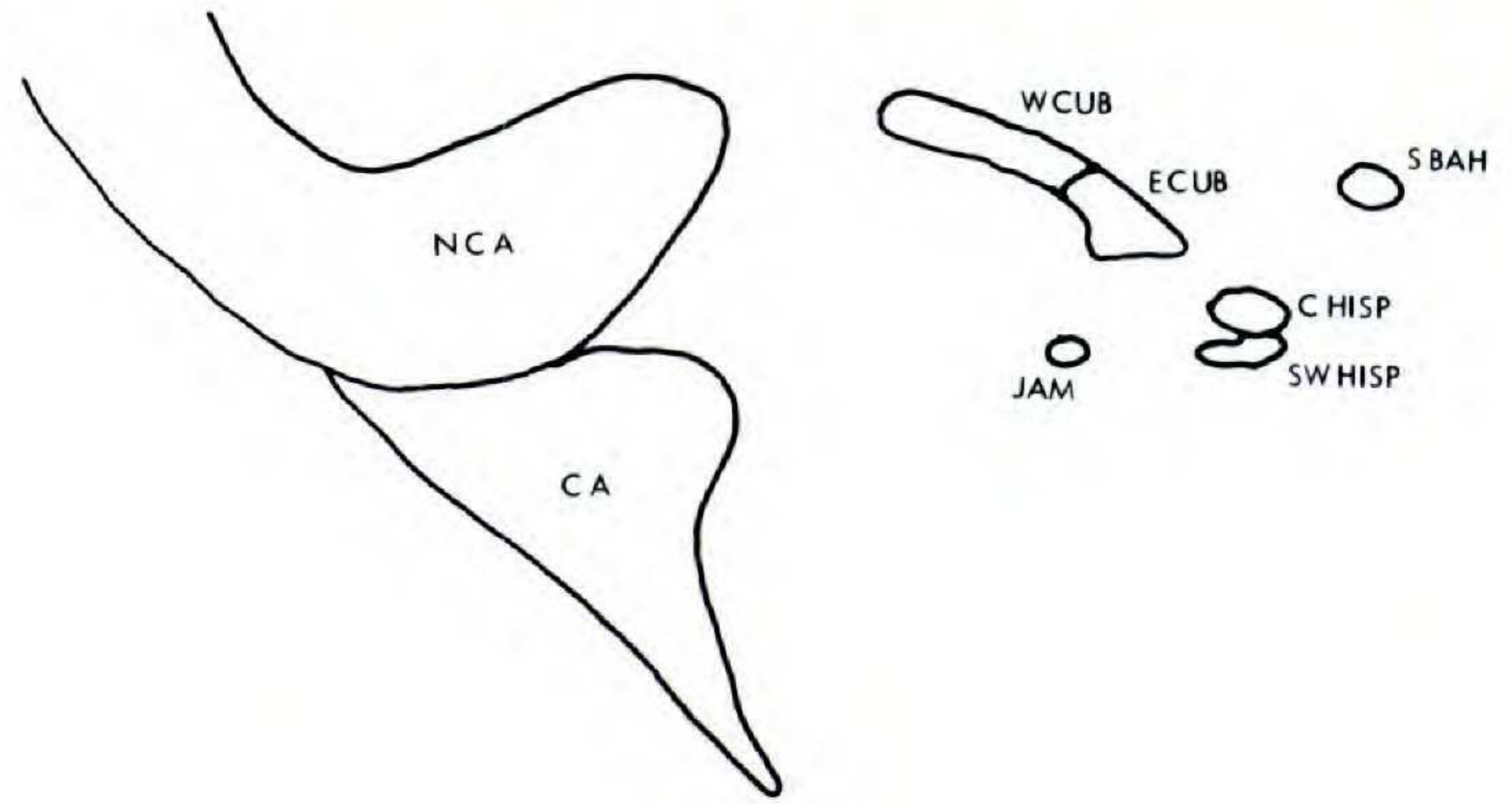
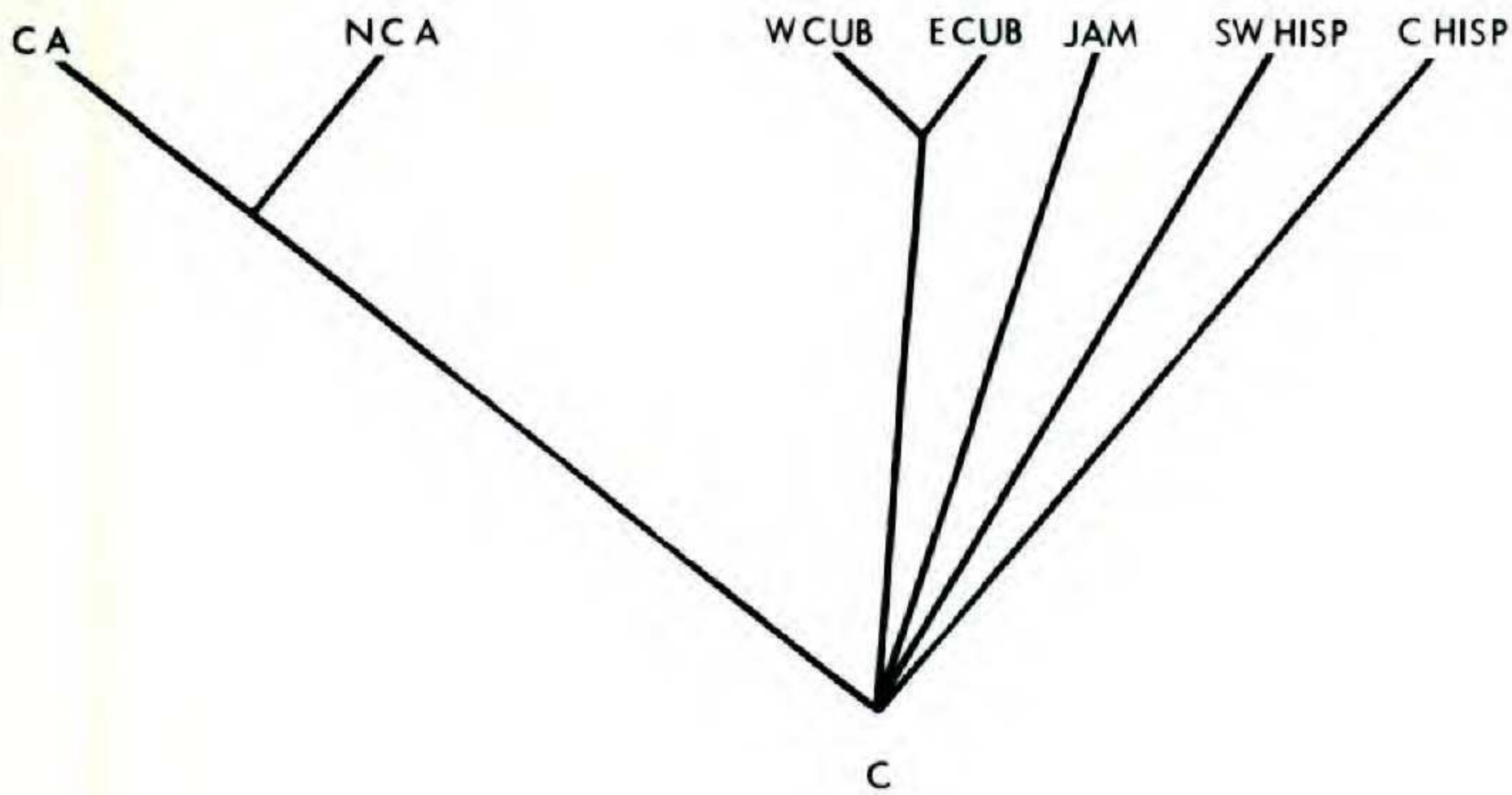


FIGURE 39. A diagrammatic consensus map of late Cenozoic relations among some main components of the Caribbean heartland and a branching diagram that summarizes these relations.



Resolved four-taxon statements derivable from C :

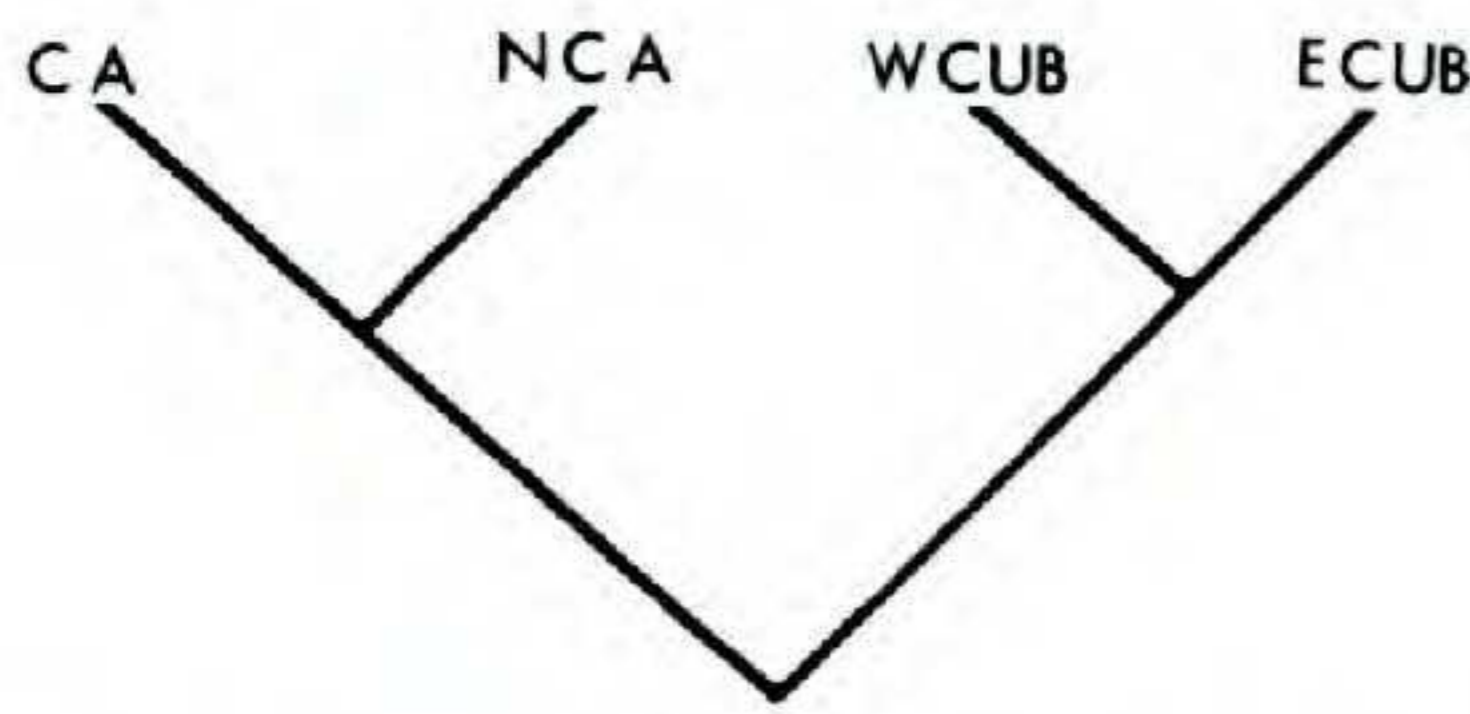


FIGURE 40. The branching diagram as in Figure 39 and the simple, completely resolved, four-taxon, four-area statement derived from it: abbreviations as in Figure 36.

paniola, and the Chortis block continues to move eastward along the Motagua-Polochic fault. The general cladogram incorporates two dichotomies, one trichotomy, and one tetrachotomy (Fig. 43), but allows derivation of seven resolved four-area statements.

The sum of all of the proposed historical geologies leads to a number of predictions:

1. Hispaniola will have a mixture of elements, some related to the Bahamas, some to eastern Cuba, some to Jamaica, and others to northern Central America (Yucatan).
2. Some of the Antillean taxa will be parts of natural groups occurring in North and South America and Africa.
3. Honduras, Nicaragua, and perhaps western Costa Rica, will share related taxa in southern and southwestern Mexico, and some of these should be parts of more inclusive taxa that include the Antilles and South America.
4. The most inclusive taxa should have representatives in all the foregoing areas and in Africa.
5. Panama and eastern Costa Rica, by and large, should share species or species groups not unique to themselves but shared with South

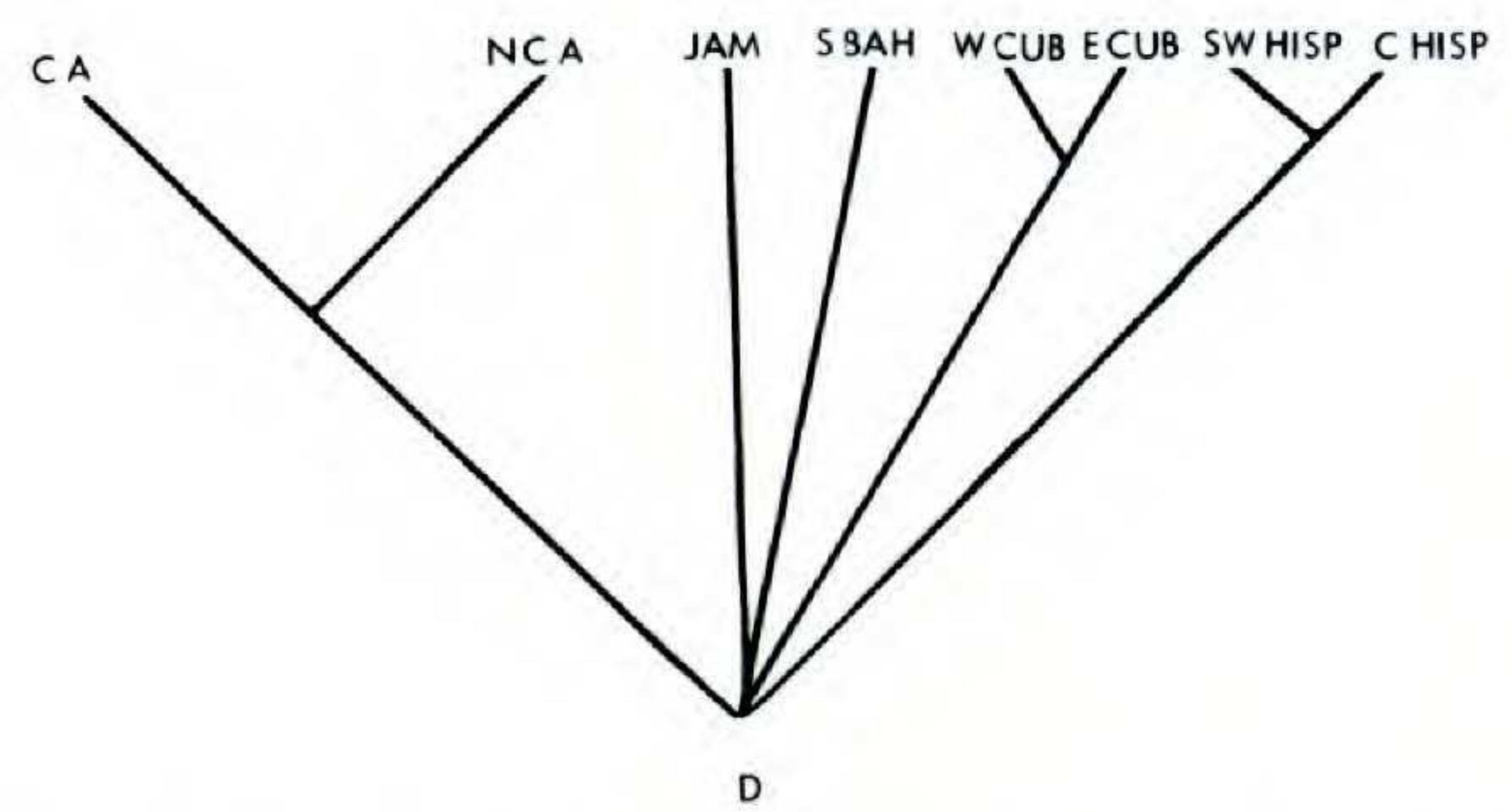
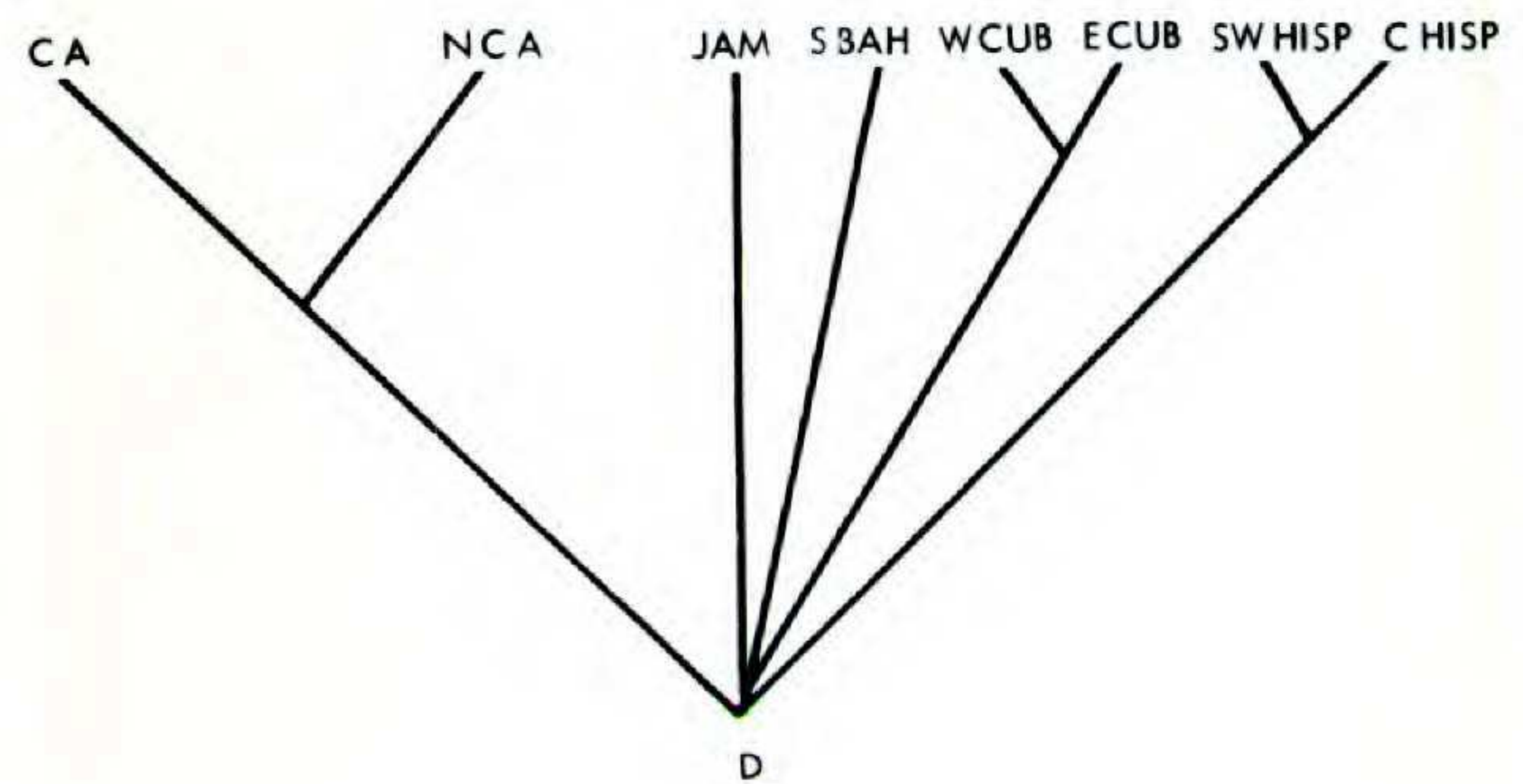


FIGURE 41. A diagrammatic consensus map of late Cenozoic relations among some main components of the Caribbean heartland and the branching diagram that summarizes these relations.



Resolved four-taxon statements derivable from D :

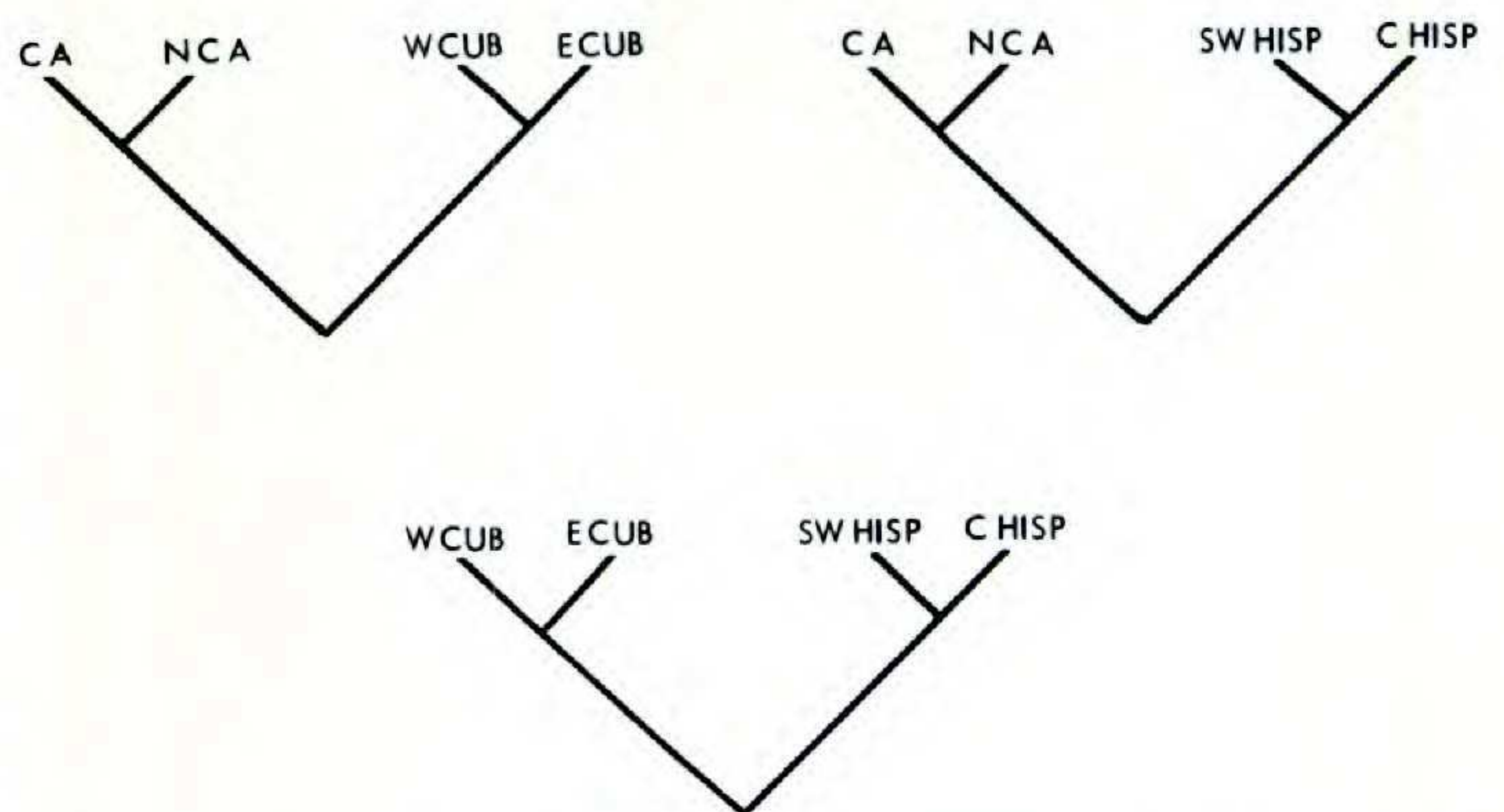


FIGURE 42. The branching diagram as in Figure 41 and the three completely resolved, four-taxon, four-area statements derived from it: abbreviations as in Figure 36.

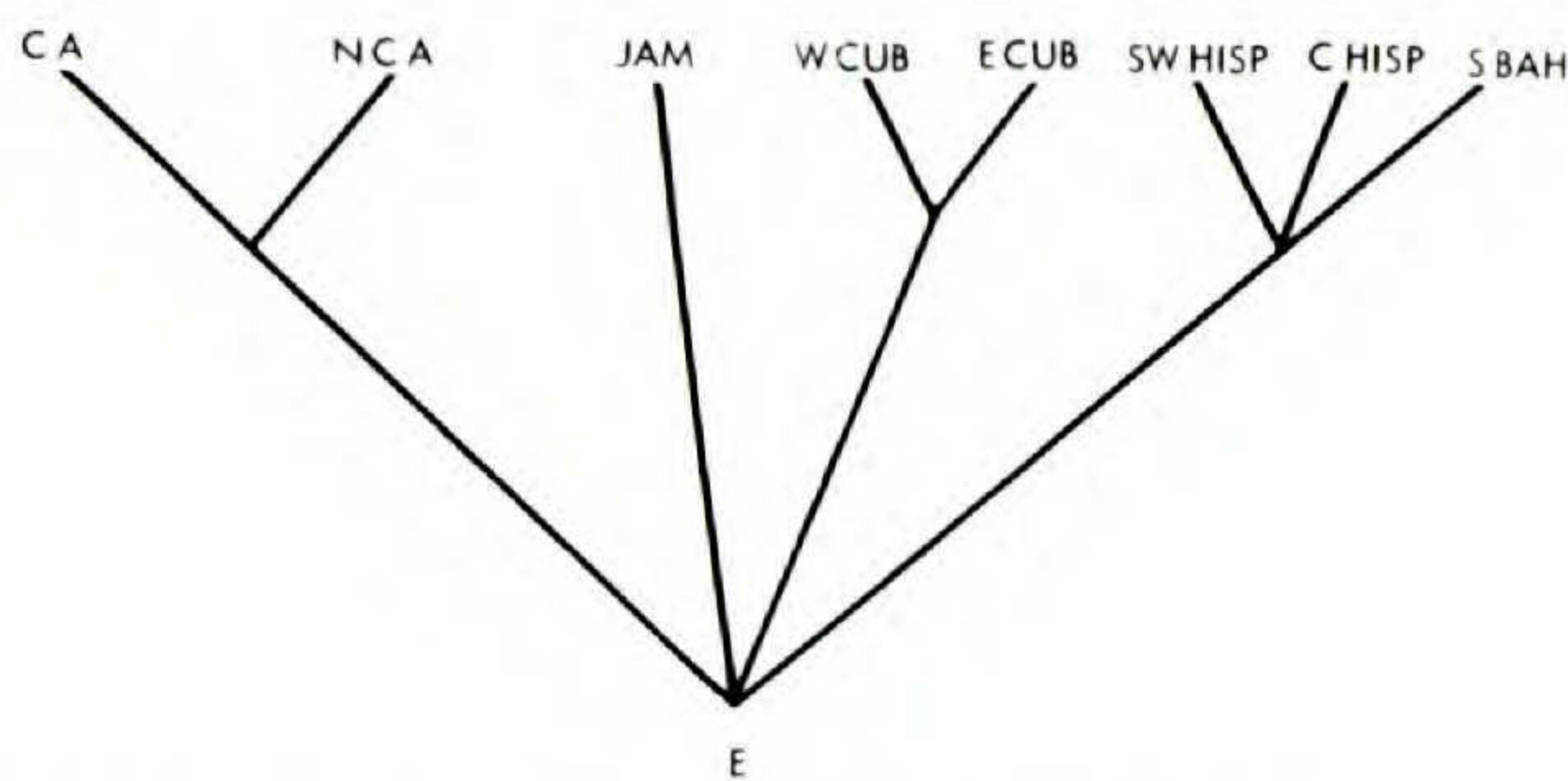
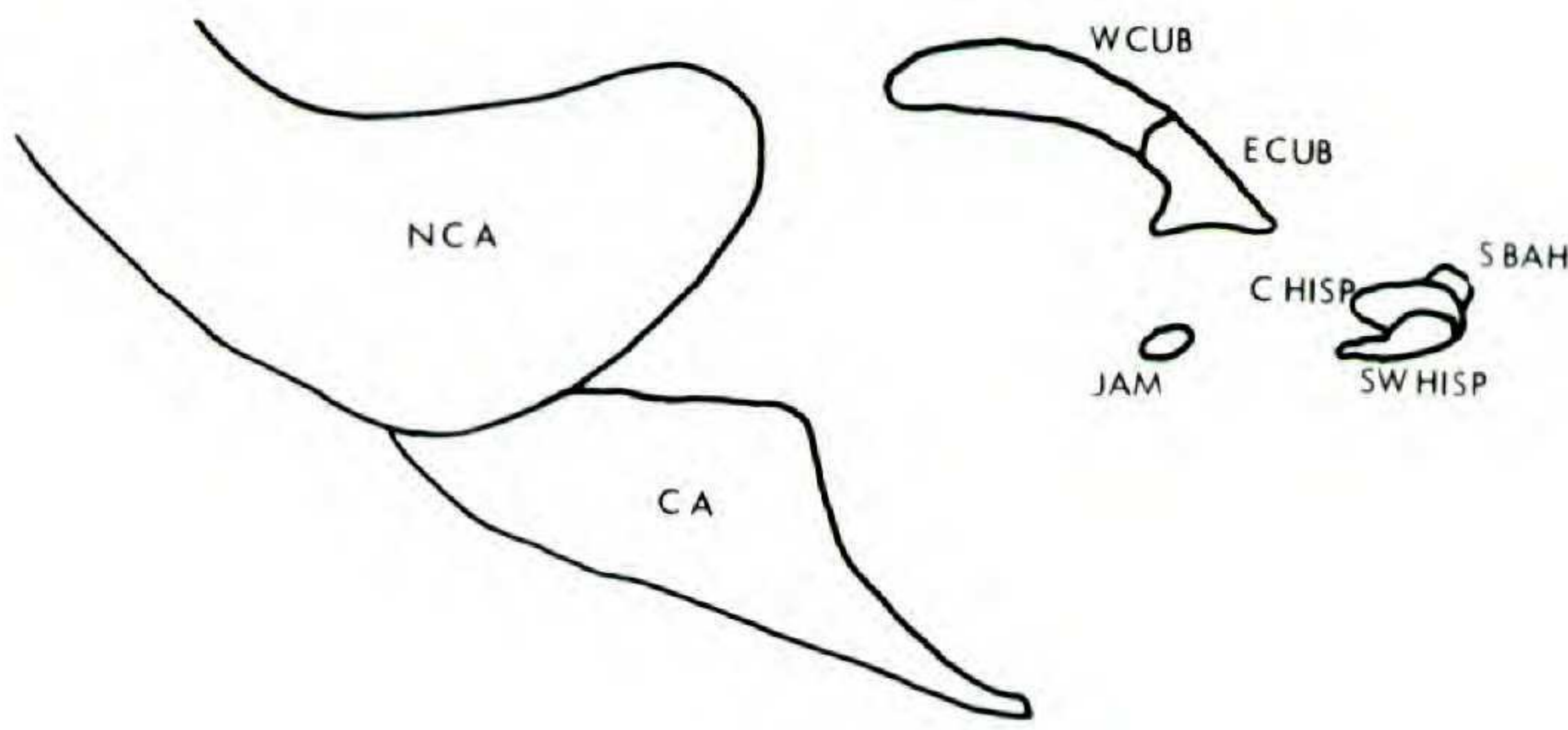


FIGURE 43. A diagrammatic map of the modern relations among some main components of the Caribbean heartland and a branching diagram summarizing these relations (SBAH, southern Bahamas).

America and southern Mexico and northern Central America (Yucatan).

- Endemic sister taxa will be found in eastern and western Cuba on each side of the uplifted Cretaceous marine deposits at about 79° west longitude.

Whether the details of this geohistory are true or false is not at issue here. What is at stake is the possibility that a geohistory of this complexity might well have occurred, meaning that there might be 19 possible four-area cladograms with which biological area cladograms can be congruent. In other words 19 different cladistic solutions to organisms' interrelationships each might reflect the dramatic events in Caribbean geohistory.

In the recent past some authors (Rosen, 1976; Tolson, 1982) have assumed that failure to discover congruence between a biological area cladogram and a single simplistic interpretation of geohistory is license to consider that some dispersal may account for the lack of congruence. Tolson (1982), for example, assumed that the occurrence on Hispaniola of three boid snakes each with a different relationship to those on Jamaica, Puerto Rico, Cuba, and the Bahamas meant that dispersal might have occurred in or-

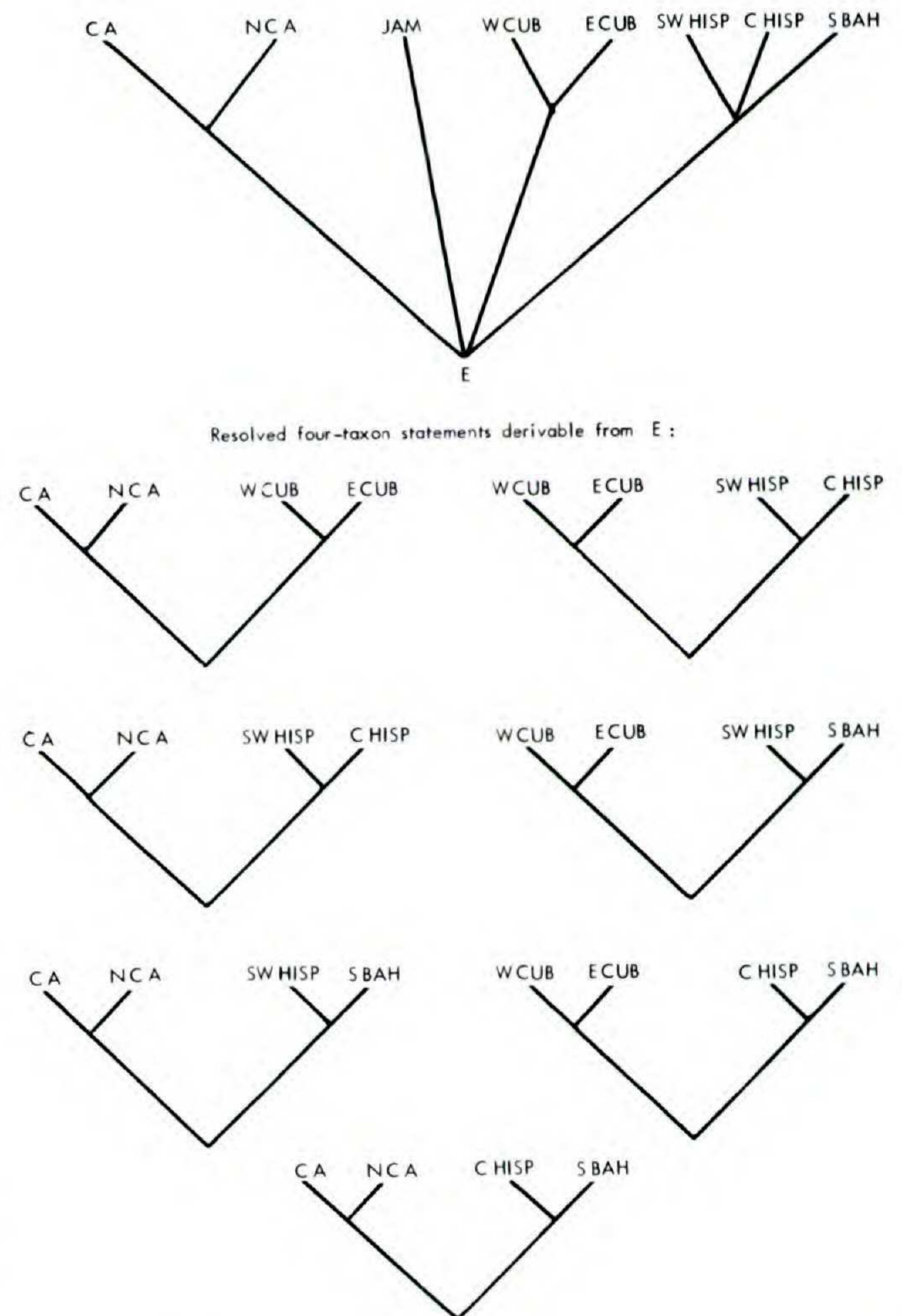


FIGURE 44. The branching diagram as in Figure 43 and the seven completely resolved four-taxon, four-area statements derived from it: abbreviations as in Figures 36 and 43.

der to permit the coexistence on one island of each of these endemics. But the complex history of Hispaniola should lead one to expect complex relationships of endemic Hispaniolan taxa.

The fact that several different historical geologies of the Caribbean specify similar kinds of complexities and support an origin of the Antilles from an ancient island arc between South America and northern Central America (Yucatan) is reason enough to suppose that land hybridization as well as fragmentation will yield a picture of unique endemism and mixed biotas in which endemic taxa from formerly isolated land fragments have been brought together in a way that conflicts with simple sister-group analysis.

There is a message here for all interested in biogeography and it is *not* that dispersal never occurs, but that theories of dispersal to explain biotic complexity are no more informative than theories of relationship based on symplesiomorphy, which widespread dispersed taxa resemble in biogeography (Nelson & Platnick, 1981).

Although geology has yet to fill in the details associated with the above five general cladograms, biology has a constructive role here because, by discovering congruent four-taxon area cladograms like the 19 derived above, it can independently support any one of the five general area cladograms and therefore details of geohistory that are still out of reach of geologists' data. If, in fact, there is a causal relation between an independent variable of geohistory and a dependent one of biohistory it should work just that way and biology should be at least as informative to the geologists as geology has been assumed to be for biologists in the past. Clearly biologists have always been ready to make that judgment since the last 150 years of biogeography has been based on the assumption that modern biotic distributions have been achieved through dispersal, signifying to geologists their belief that the relevant part of geohistory has been one of stabilism—a view that could have been challenged only by a theory of plate tectonics or a biological theory of general area congruence as proposed by Leon Croizat (1958, 1962).

In such detailed historical summaries of the geology of a region there is an unfortunate air of real knowledge, but Weyl (1980) has warned that, not only does the problem of reconstruction become increasingly difficult as we go back in time, but that the only criteria we have to go by are the data of prehistoric magmatism and the structure of the uppermost part of the crust, while the seismic and gravimetric data that are so important either are lacking or are poorly known relative to what is needed for establishing a detailed historical picture.

Even though one of the most detailed recent historical geologies (Sykes et al., 1982) is based on the paleoseismic data required by Weyl, biological data from the living and fossil biotas might have still more to say about Caribbean history. For example, if each of the 19 resolved four-taxon area cladograms were corroborated by a significant amount of taxonomic evidence, that general congruence would establish that the foregoing account was, indeed, the most probable geographic history of the region. But to accept as true the proposals of one geological model, and to abandon the search for cladistic area-congruence in favor of some a priori notion that all distributions might be explained by guesswork liberally laced with dispersalist intuition is to ensure that future generations of biogeographers will regard such proposals lightly. The fact that

there are 19 resolved four-area cladograms that need to be corroborated might seem somewhat daunting to someone venturing for the first time into cladistic biogeography because it will, indeed, require a stupendous multidisciplinary effort to resolve decisive patterns for the region—and more still if one adds Mexico, North and South America, and Africa.

But I presume that if the problem were less difficult there would have been fewer attempts to describe nature by casual dispersalist scenarios about which almost no two scenario-writers can exactly agree, or provide that decisive constraint that shows one or another scenario to be flawed and scientifically unacceptable. But the history of today's biogeography has been characterized by the casual, almost offhand, manner of the scenario-writers that populate the field. Nevertheless, the temptation to propose imprecise, non-cladistic, solutions to the problem of Caribbean history is great because of the abundance of endemic taxa that link certain areas. Patterson (1981: 458) complained that these seemingly reassuring biogeographic data add up to a phenetic concept that cannot lift biogeography out of its present narrative phase.

But all problems in comparative biology begin with a data gathering phase that incorporates unknown amounts of noise and signal. Cladistics identifies the signal. The need for cladistic vicariance analysis is underscored by questions such as those following.

How significant is the co-occurrence on Hispaniola of boid snakes in relation to a geological theory of a threefold origin for Hispaniola?

How significant is the occurrence of swamp eels of the genus *Ophisternon* restricted to Trinidad, Cuba, and northern Central America north of the Chortis block?

How significant are the occurrences of *Carlhubbsia* and *Quintana* plus *Girardinus* in northern Central America (Yucatan) and Cuba respectively (Rosen & Bailey, 1959) in relation to theories of ancient connections between western Cuba and the Yucatan?

How significant is the occurrence of related taxa of the poeciliid genus *Gambusia* in Cuba, the Bahamas, Hispaniola, and northern Central America (Yucatan) in relation to mid-Cenozoic interconnections of these areas?

These distributions, linking disjunct or hybrid areas, appeal to our sense of discovery. A cladistic analysis of areas will help us decide whether the distributional components that drew our

attention specify a general problem. I predict that such analysis, on a grand scale involving many different kinds of organisms, will corroborate some, if not all, of the five general geological area-cladograms that describe the longitudinal displacement theories of Caribbean history of Pindell and Dewey (1982), Sykes et al. (1982), and Wadge and Burke (1983). But, if such corroboration is not forthcoming, as biologists we are bound by the message of biological data in describing a biotic history of those geographic areas regardless of any possible conflicts with geologic theory.

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